The Influence of Rainfall Variability on Savanna Tree Seedling Establishment

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Abstract

My thesis investigates the rainfall requirements necessary for tree seedling survival of different savanna species in the first year of growth. Results from a field drought experiment showed that dry season survival for seedlings of *Acacia nigrescens* and *Philenoptera violacea* was not related to wet season length. Instead mortality was highest immediately after germination despite irrigation to minimize dry spells. Furthermore there was no relationship between seedling size and the length of the dry spell seedlings of *Acacia nigrescens* and *Philenoptera violacea* grown in basalt clay in the greenhouse, could survive. This was in contrast to seedlings of *Sclerocarya birrea* and *Terminalia sericea* grown in granite sand, where number of dry days survived increased with number of growth days received. There was no significant differences in rainfall variability (t-test: $t_{1,\ 111} = 1.56$, $p = 0.121$, F-ratio = 1.13) between a semi-arid (Satara) and semi-mesic (Pretoriuskop) site within the Kruger National Park despite significant differences in rainfall totals (t-test: $t_{1,\ 111} = 4.40$, $p < 0.000$, F-ratio = 3.41). Results from a soil-water model show that seedling recruitment can occur at least twice a decade in the Satara area, which should be frequent enough to allow a transition to a woodland state over time. These results suggest that a mechanism other than the effect of rainfall variability on seedling establishment is required to explain the co-existence of trees and grasses at Satara. The lack of field germination, the absence of a seed bank and the germination of added seed at the field experiment site after rainfall emphasizes seed limitation as an important bottleneck at Satara. Higher herbivore biomass at Satara compared to Pretoriuskop may limit seedling establishment opportunities by destroying seed and seedlings of tree species.

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Chapter 1

Introduction

Savannas are characterized by having a discontinuous tree and continuous herbaceous layer. Although tree cover can vary widely (Medina & Silva, 1990), vegetation physiognomy of savannas can be differentiated from forest and grassland. Much research in savanna systems has investigated what prevents trees, or alternatively grasses, from thickening over time to form a woodland or grassland (Sankaran *et al.*, 2004) since this aids in the maintenance of the savanna "state", that is, a co-existence between grasses and trees.

Models that explore the mechanisms that drive co-existence of trees and grasses in savannas have suggested sufficient availability of water as a critical bottleneck to tree seedling survival. The "Root-Niche Separation Model" (Walker & Noy-Meir, 1982; Walter, 1971) argues that trees and grasses co-exist because they occupy different rooting zones which eliminates competition for water. This implies that the tree seedling stage is the most vulnerable since tree seedling roots still need to penetrate through the grass-root layer and are therefore in direct competition with grasses for water (Walter, 1971). Seedling establishment is more likely in above-average rainfall years where competition for soil moisture with grasses is reduced. Some evidence supports the idea that grass competition inhibits seedling establishment (Gordon, 1989; Harrington, 1991). In many cases competition with grasses does not limit tree density (Brown & Archer, 1999; Chirara, 1989; Davis, 1999; O'Connor, 1995; Scholes & Archer, 1997) and competition only becomes important when water supply is insufficient (Davis, 1999; Harrington, 1991; O'Connor, 1995).

Recently the "Demographic Bottleneck Model" proposed that the transition towards a woodland state is prevented in xeric savannas by extended dry periods within the wet season limiting tree seedling survival (Higgins *et al.*, 2000). Conversely in mesic savannas, more frequent suitable rainfall distribution within the wet season allows frequent tree seedling establishment. Here co-existence is driven by more frequent fires that keep saplings trapped within the fire zone (Higgins *et al.*, 2000). Competition between tree seedlings and grasses has received much attention. The

influence of rainfall amount and distribution on seedling survival has however not yet been studied. We still don't know how important the seedling recruitment stage is in limiting populations of savanna trees relative to subsequent life history stages. Is seedling recruitment more probable in mesic savannas so that this life history stage is not an important bottleneck for mesic savannas (Higgins *et al.,* 2000)? How often are the rainfall conditions required for suitable seedling establishment fulfilled, once every ten years, or once every 100 years? Does this differ vastly between different species, and if so, why? Is it possible to predict likely recruitment years as a guide to managing savannas?

My thesis investigates the rainfall requirements for survival of tree seedlings of different savanna species in the first year of growth. It also examines how frequently this has been fulfilled in the past. I test whether extended dry spells within the wet season increase with decreasing rainfall (Higgins *et al.,* 2000) for a semi-arid (Satara) and semi-mesic (Pretoriuskop) site within the Kruger National Park. Comparing rainfall characteristics between the two sites I also determine whether rainfall conditions suitable for germination and seedling survival have occurred more frequently at the semi-mesic versus the semi-arid site (Higgins *et al.,* 2000).

It has been implied that seedlings that maximize the length of the first growth period to accumulate root reserves have a better chance of surviving the subsequent dry season (Medina & Silva, 1990). Trees supposedly drop their seeds towards the end of the dry season so that seedlings can germinate with the first rains, thus enabling utilization of the full growing season (Williams, 1999). A study of desert succulents showed that the survival of seedlings during the dry season was related to the length of time seedlings had to grow water-storing leaves during the preceding rainy season (Jordan & Nobel, 1979). Here I test (Chapter 4) whether a similar relationship between the length of the wet season and survival of the dry season exists for savanna tree seedlings. For certain savanna species it has been shown that germination is higher under higher (less negative) soil moisture potential (Choinski & Tuohy, 1991) and at the highest irrigation regimes (Bebawi & Mohamed, 1982). Little is known about the actual timing of germination in the field, which may influence the chances of seedlings surviving the dry season (Jordan and Nobel, 1979). Therefore I

investigate field germination at Satara and Pretoriuskop in the Kruger National Park (Chapter 4).

I also test whether different species have different drought tolerances since this should influence their recruitment intervals. Species that are more common in arid savannas may be better adapted to drought and therefore, in contrast to the suggestions by Higgins *et al.,* (2000), be able to establish as frequently as species that are widespread in mesic savannas. I also test whether Satara has a larger persistant seed bank compared to Pretoriuskop (Chapter 4). A persistant seed bank may be more prevalent in the semi-arid area where risk-spreading of germination has a higher adaptive advantage compared to the semi-mesic area (Clauss & Venable, 2000). This strategy, known as bet-hedging, is common in desert annuals where only a proportion of the persistant seed bank germinates every year and germination within a rainy season is spread over several rainfall events.

I conducted a greenhouse study to test how dry spells within the rainy season influence seedling survival (Chapter 5) since this has been suggested to limit seedling survival (Wilson & Witkowski, 1998). I supplied water for different periods after initial germination and then recorded survival rates of four different species after watering ceased.

Finally, I wanted to determine how frequently seedling establishment can potentially occur at Satara and Pretoriuskop by combining past rainfall records with a soil-water model (Chapter 6). I also wanted to determine how the hydraulic properties of a soil coupled with rainfall may influence seedling establishment opportunities. Many arid savannas are characterized by having clay soils that have high water retaining capacities. However because of the properties of the soil less of the water is available for plant uptake. In contrast, sandy soils often common to mesic savannas have low water holding capacity but more of the water is available to plants (Wild, 1988).

The final chapter (Chapter 7) concludes by summarizing the results and discussing the importance of rainfall variability in limiting savanna tree populations.
The outline of my thesis is as follows:

- **Chapter 1:** Introduction
- **Chapter 2:** Description of my study site: Kruger National Park.
- **Chapter 3:** I investigate whether rainfall conditions suitable for seedling establishment have historically occurred more frequently at Pretoriuskop (semi-mesic) compared to Satara (semi-arid).
- **Chapter 4:** I investigate whether a longer growing season increases dry season survival for different savanna species. I investigate the timing of germination for different tree species and the presence of a seed bank at Satara and Pretoriuskop. I also investigate seedling morphological adaptations of different species to drought stress.
- **Chapter 5:** I investigate how dry spells within the wet season influence seedling survival for four different savanna tree species.
- **Chapter 6:** I determine the likely recruitment frequencies for seedlings at Satara and Pretoriuskop using past rainfall records, seedling requirements for establishment, and a soil moisture model to explore how frequently these were met in a given year.
- **Chapter 7:** Conclusion.
- **Appendix A:** Description and values of the parameters used in the soil-water model.

Chapter 2

Study Area

The Kruger National Park forms part of the north-eastern South African lowveld, a low-lying area between the extensive Mozambican coastal plain to the east and the Drakensberg Escarpment to the west (Fig. 1)(Coe & Coe, 1987; du Toit *et al.*, 2003). The lowveld area forms part of a broad landform pattern, the Eastern Plateau Slope, and consists mainly of plains with low to moderate relief. The Kruger National Park is subdivided roughly into two broad geological types that separate the park into two halves; granitic rocks in the west and basaltic rocks in the east (Fig. 1). Rainfall generally decreases from the south (700 mm) to the north (450 mm) (Venter & Gertenbach, 1986). Soil profiles follow a similar trend, decreasing in depth from the south (1-3 m) to the north (0.5 – 1m) of the park, especially for coarse-grained soils derived from granitic material (Venter & Gertenbach, 1986). The soil type and associated rainfall pattern influences the vegetation found in different parts of the park (Venter & Gertenbach, 1986). The nutrient-poor granite or sandstone-derived substrates tend to be dominated by deciduous, broad-leaved species with no thorns from the families Combretaceae (especially *Combretum* and *Terminalia* spp.) and Caesalpiniaceae. The more nutrient-rich clay soils are dominated by species from particularly the Mimosaceae (especially *Acacia* spp.) that are deciduous, with fine compound leaves and thorns (Venter & Gertenbach, 1986).

The climate of the Kruger National Park is influenced by anticyclonic systems moving semi-rhythmically over southern Africa from west to east. During the summer months extremely hot and dry conditions are created by the presence of anticyclonic conditions in the interior. After a period of these hot and dry conditions, a low pressure cell usually develops over the interior, resulting in an influx of warm, moist air from the north and north-east, which often results in convective thunderstorms, which delivers most of the rain (Venter and Gertenbach, 1986).

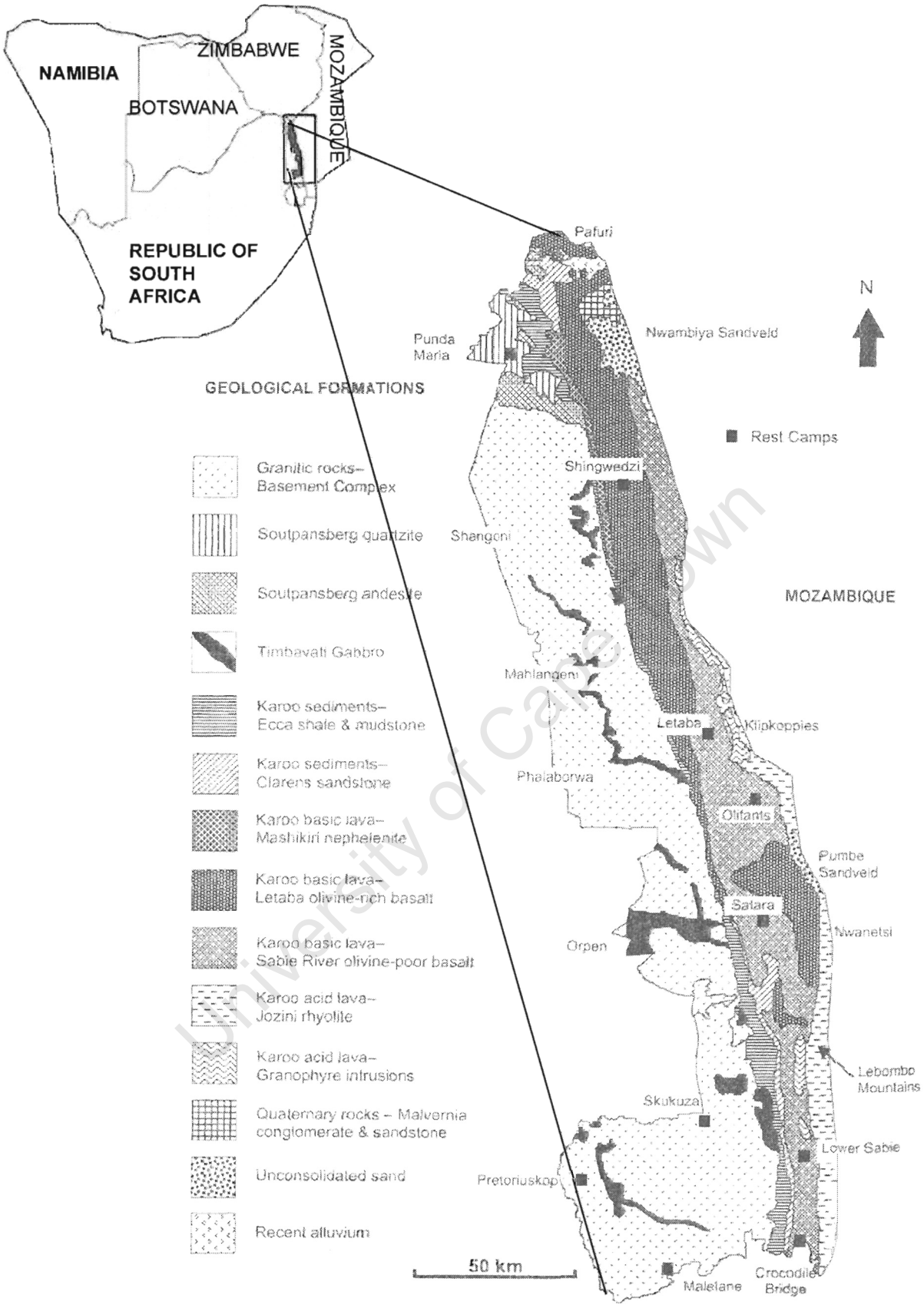

Figure 1 A map of the Kruger National Park depicting the broad underlying geology of the different areas.

Over the winter months anticyclonic conditions usually preside over the interior of South Africa which results in fine and mild conditions over the Lowveld (Venter & Gertenbach, 1986). Approximately twice monthly cold frontal systems of polar origin penetrate from the south leading to windy and overcast conditions and occasional light drizzle. Occasionally tropical cyclones occur during the late summer months (Venter & Gertenbach, 1986). These originate in the equatorial areas of the Indian Ocean when the surface sea temperatures rises above 27°C, moving slowly down the Mozambique Channel and depositing large amounts of rainfall within a few days (du Toit *et al.,* 2003). These events are usually characterized by flooding and destruction of roads and bridges (Venter & Gertenbach, 1986).

There is no clear tendency for annual rainfall to be either increasing or decreasing over the past seventy years for both sites (Fig. 3).

Site Descriptions

For the purposes of this study I compared the semi-mesic area of Pretoriuskop with the semi-arid Satara area (Fig. 1). For the drought field experiment Lower Sabie was chosen as a substitute site to that of Satara because it reduced the commuting distance between the semi-mesic site and the semi-arid site. Satara (Temperature: yearly average 22.83 °C; Rainfall: yearly average 580 mm) and Lower Sabie (Temperature: yearly average 23.40 °C; Rainfall: yearly average 589 mm) have basalt clay soils (Fig. 1) and similar temperature regimes (Fig. 2). Both Satara (altitude = 275m), Pretoriuskop (Temperature: yearly average 21.67 °C; Rainfall: yearly average 793 mm) (altitude = 600m) and Lower Sabie are characterized by high mean temperatures (Fig. 2)) in summer and mild generally frost-free winters (du Toit *et al.,* 2003). Temperature and rainfall is seasonal for all three sites (Fig. 2).

The nutrient-rich soils of Satara support fine-leaved tree species, particularly *Acacia nigrescens,* whereas the Pretoriuskop area support broad-leaved tree species dominated by *Terminalia sericea.*

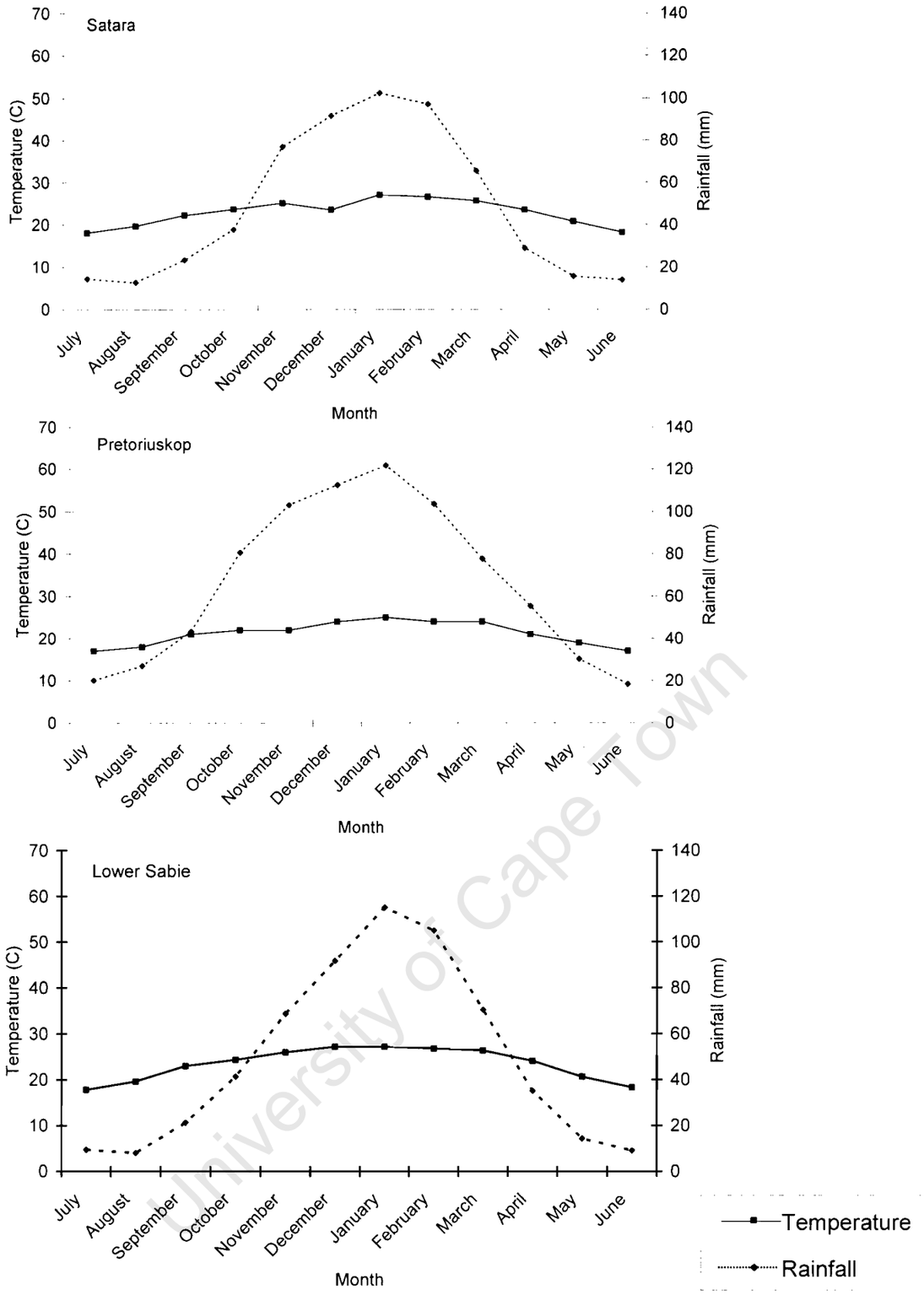

Figure 2 The average monthly temperature (°C) and rainfall (mm) for Pretoriuskop, Satara and Lower Sabie.

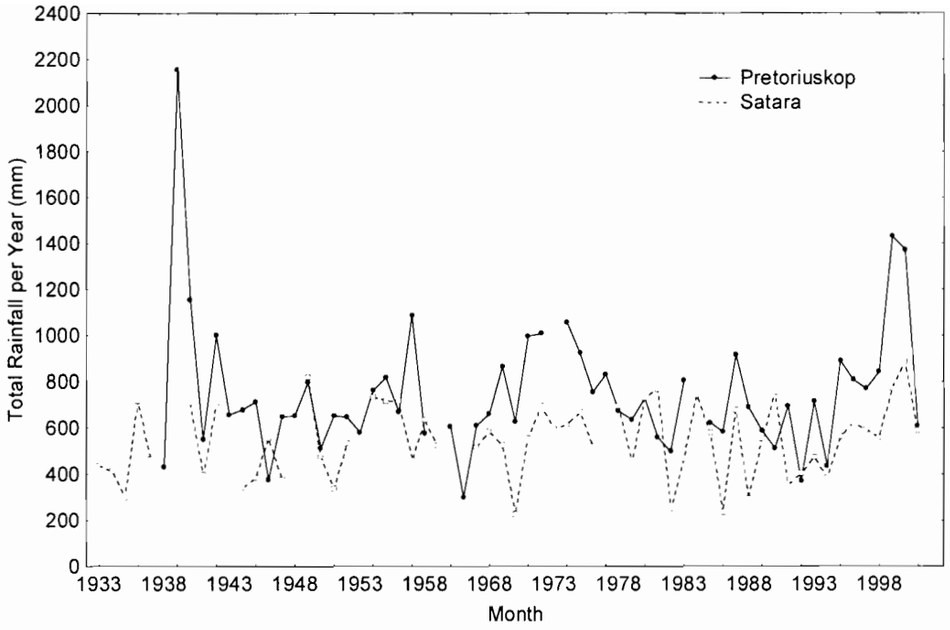

Figure 3 The total precipitation (mm) per year for Pretoriuskop and Satara from 1933 to 2002. Years with more than four days of missing data were omitted.

Chapter 3

Can the temporal distribution of rain explain the co-existence of trees and grasses for two sites in the Kruger National Park?

Abstract

Increased rainfall variability has been suggested to promote the co-existence of trees and grasses in semi-arid and arid savannas. This is because increased more frequent dry periods within the rainy season with declining rainfall should limit the establishment opportunities of savanna tree species. I tested the assumption that rainfall variability should increase with decreasing annual rainfall and other rainfall characteristics to determine whether seedling establishment is more likely at a semi-mesic (Pretoriuskop) compared to a semi-arid (Satara) site within the Kruger National Park. I found no significant difference in rainfall variability (t-test: $t_{1,\ 111} = 1.56$, $p = 0.121$, F-ratio = 1.13) between the two sites despite significant differences in rainfall totals (t-test: $t_{1,\ 111} = 4.40$, $p < 0.000$, F-ratio = 3.41). There was no difference in the length of the wet season between the two sites and Pretoriuskop experienced slightly longer consecutive dry periods within the wet season compared to Satara. Both sites also had similar probabilities of receiving a large rainfall event to stimulate germination and follow-up rainfall. These results suggest that a mechanism other than rainfall effects on seedling establishment is required to explain the co-existence of trees and grasses at Satara. Higher herbivore biomass at Satara compared to Pretoriuskop may limit seedling establishment opportunities by destroying seed and seedlings of tree species.

Introduction

Variability in the temporal distribution of rainfall within the rainy season has been suggested to limit the establishment success of newly germinated seedlings (Hoffman, 1996; Keya, 1997; Veenendal et al., 1995). In line with these ideas, output from the "tree demographic model" of Higgins *et al.,* (2000) predicts that tree seedling establishment should occur more frequently in mesic compared to semi-arid savannas. The input parameter pertaining to seedling establishment frequencies for the "tree demographic model" is based on the assumption that savanna tree seedlings are unable to survive long continuous dry spells within the wet season, a period longer than 30 days. It is further assumed that the probability of experiencing a 30-day dry spell increases with decreasing rainfall (Higgins *et al.,* 2000). This results in a higher occurrence of tree seedling establishment events in mesic than in xeric savannas (Adiku, 1997; Higgins *et al.*, 2000).

However the assumption that rainfall variability increases from mesic to xeric savannas may not be a valid one to make. Davidowitz (2002) showed that rainfall variability is highly dependant on site location; certain desert sites included in his analyses were no more variable that sites from grassland or pine forest biomes across a rainfall gradient in the South-western United States. His results suggest that broad generalizations of rainfall variability based on annual rainfall alone can be erroneous as site conditions need to be considered (Davidowitz, 2002).

The assumption that seedlings can not survive longer than thirty no-rain days during their first wet season (Higgins *et al.,* 2000) may be adequate for simulation models but has a slim ecological foundation. Small-sized seedlings show greater mortality compared to bigger-sized seedlings (Gilbert et al., 2001). This suggests that seedlings should be more at risk of succumbing to an extended dry spell immediately after germination compared to seedlings that have had a longer period to grow within the wet season (Jordan & Nobel, 1979). For this reason, it has been suggested that adult trees drop their seeds at the end of the dry season/ start of the wet season so that seeds could germinate with the first rains (Khurana & Singh, 2001; Williams, 1999). This

strategy could enhance seedling survival in the subsequent dry season since these seedlings have utilized the entire wet season's rainfall to develop root resources.

If the length of the wet season determines dry season survival (Jordan & Nobel, 1979), seedling establishment may be more frequent in mesic savannas. In the Kruger National Park (KNP) the wet season period falls between November and March (Venter & Gertenbach, 1986). This broad scale definition of the wet season assumes that wet season length is equal across the xeric and mesic regions of the KNP (du Toit *et al.,* 2003). However ecological processes like leaf flush and seed production of adult trees have been observed to occur later in the more xeric compared to the more mesic regions of the KNP (*own, unpubl. data*).

Similarly the timing of ecological processes varies along a rainfall gradient in the tropical savannas of northern Australia (Cook & Heerdegen, 2001). These observations drove Cook & Heerdegen (2001) to define the wet season on different climatic criteria as that of the length of the monsoon. They defined the length of the wet season as the period when the probability of a 10-day dry spell was less than 0.5 and the wet season as the period within the rainy season where the probability of a 10-day dry spell was less than 0.1. This definition corresponds to many ecological patterns such as deciduous tree leafing (Cook & Heerdegen, 2001). It also showed that the length of the wet season decreases along a rainfall gradient of 1200 mm to 200 mm. Defining the length of the wet season based on such climatic criteria as that of Cook & Heerdegen (2001) may be more insightful in predicting the start and length of the growing season across a rainfall gradient in the KNP. More xeric regions may have shorter wet seasons compared to the more mesic regions and given that seeds germinate with the first rains, seedling establishment may thus be more frequent in the mesic regions (Jordan & Nobel, 1979).

The soil profile is at its driest at the end of the dry season and therefore rainfall that stimulates germination at the start of the wet season may not be adequate to wet the soil deeply enough for initial root growth. If plant species respond to cues that stimulate germination at the start of the wet season, it would require a rainfall event large enough to wet the soil deeply enough for initial root growth or alternatively follow-up rainfall would be essential. Savanna seeds are adapted to germinate after

heavy rainfall events (Barnes, 2001) and experimental studies report soaking seeds for a period of time enhances germination (Choinski & Tuohy, 1991; Wilson & Witkowski, 1998). Laboratorial studies have also shown that germination for savanna species only occurs under the highest irrigation regimes (Bebawi & Mohamed, 1982; Wilson & Witkowski, 1998). Although these greenhouse and petri dish experiments are indicative of the rainfall conditions required for germination it is not known when and how frequently these conditions are met in the field. Alternatively, if rain days increases with annual rainfall and presuming number of rain days are regularly spaced apart across a rainfall gradient, germination success after a small rainfall event should increase with increasing rainfall. This is because, as the number of rain days increases with increasing rainfall the higher the probability would be to receive a rain day after germination.

Seedling establishment requires not only sufficient rainfall to stimulate germination but also sufficient rainfall to ensure seedling survival (Hoffman, 1996; Wiegand *et al.*, 2004; Wiegend *et al.*, 2004; Wilson & Witkowski, 1998). It is the synchrony of these two requirements that seemingly make seedling establishment a rare event. The probability of the combination of rainfall events to stimulate germination and survival has also been used to predict the probability of successful seedling establishment events across years (Wiegand *et al.*, 1995). Presuming that the number of rain days increases with annual rainfall and the number of rain days are regularly spaced across a rainfall gradient, annual rainfall could be used as an indicator of seedling establishment success. This is because as the number of rain days increase with increasing rainfall the higher the probability of receiving rain after germination.

In this chapter I analyze rainfall distribution for two sites (Chapter 2) within the KNP with different annual rainfall to test whether seedling establishment opportunities should increase with rainfall (Higgins *et al.,* 2000). The aim of the study is to characterize inter- and intra-annual variability in rainfall and implications for timing of germination and seedling establishment. Specifically I ask i) is rainfall variability higher at the xeric (Satara) compared to the mesic (Pretoriuskop) site? (ii) Is there a relationship between the number of rain days and total annual rainfall? (iii) Does Pretoriuskop have a longer wet season compared to Satara? (iv) How frequently does

the right rainfall conditions for germination and survival (seedling establishment) occur and does this differ between Pretoriuskop and Satara?

To answer the first question (i) is rainfall variability higher at Satara compared to Pretoriuskop I use the Levene's test of homogeneity of variance to test whether Satara has more variable annual and monthly rainfall than Pretoriuskop. To address the second question (ii) I correlate annual rainfall with annual number of rain days for Satara and Pretoriuskop respectively. For the third question (iii) whether wet season length is different between Satara and Pretoriuskop I use the climatic criteria employed by Cook & Heerdegen (2001). The rainy season for Satara and Pretoriuskop is defined as the period when the probability of a 10 and 30 day dry spell was less than 0.5 and the wet season as the period within the rainy season where the probability of a 10 and 30 day dry spell was less than 0.1.

For the final question (iv) how frequently do the right rainfall conditions occur and does this differ between Pretoriuskop and Satara I defined different "rainfall combinations" necessary for germination and seedling survival. I then calculated the probability of these occurring throughout the months of September to April for both Satara and Pretoriuskop. The number of rainfall combinations that can be calculated is limitless and here I present a subset of combinations that provide useful insights into the wet season distribution of rainfall necessary for germination and establishment. The combinations are based on two rainfall requirements: firstly, enough rain is needed to trigger germination and secondly, subsequent rainfall within a given amount of time is needed to ensure survival. Based on these criteria, I calculated the probability of certain "rainfall combinations" (or "events") occurring throughout the wet season (from September to April). The rainfall "events" consist of three parts: 1) the size of the first rainfall event, 2) the number of days following the event and 3) the subsequent rainfall within a specified number of days after the first event. A 10.15.30 rainfall "event" would then refer to the probability of any month receiving 30 mm of rainfall within 15 days of a 10 mm rainfall event.

Methods

Rainfall records and statistical analysis

Rainfall records were obtained from Kruger National Park Scientific Services (Nick Zambatis, *pers. comm.*). These are more complete than the records from the South African Weather Bureau since missing records from the weather stations are supplemented with records kept by the regional game ranger. Rainfall years with more than four days of missing records were omitted from the analyses. For years with less than four days of missing records, it was assumed that no rain fell on those days. For Pretoriuskop, records span from 1938-1958; 1964-1965; 1967-2003 and for Satara, from 1933-1937; 1940-1942; 1944-1947; 1949-1952; 1954-1959; 1967-1976; 1978-2002.

Levene's test of homogeneity of variance

The among-year coefficient of variation (CV) of total annual precipitation is the most frequently used measure of precipitation variability in ecological studies. This measure has been shown to be a biased estimator of variation in positively skewed samples, which is typical of precipitation data (Davidowitz, 2002). Removing a single point (1939) from the Pretoriuskop data set reduced the average annual CV of precipitation from 40% to 32%. I therefore decided to use the Levene's statistic instead which is commonly used in ANOVA to test the assumption of homogeneity of variance. However instead of performing an analysis of variance on the values of absolute deviations of the group means it was used to measure absolute deviations using the median as a measure of central tendency (Davidowitz, 2002). The results from the Levene's statistic (Davidowitz, 2002) are reported as AYV (annual yearly variation) and AMV (among month variation).

Annual yearly variation was measured as:

$$Y_j = \frac{\sum_{i=1}^{n_j} \left| \log_{10}(x_{ij}) - Md_{j\log_{10}(x_i)} \right|}{n}$$

where Y_j (Levene's test) is the total annual among-year precipitation variability of weather station *j*, $\log_{10}x_{(ij)}$ is the logarithm of the total annual precipitation for year *i* for weather station *j*, and *n* is the total number of years of data for weather station *j*. This measure is the among-year average of the absolute deviations of the total annual precipitation from the among-year median for each weather station (Davidowitz, 2002)

The among-month, within-year variability (AMV) was calculated as:

$$M_r = \frac{\sum_{p=1}^{n} \left[\frac{\sum_{q=1}^{12} \left| \log_{10}(x_{qp}) - Md_{p\log_{10}(xq)} \right|}{12} \right]}{n}$$

where M_r is the among-months, within-years variability for weather station *r*, $\log_{10}(x_{qp})$ is the total monthly precipitation for month *q* of year *p*, $Md_{p\log_{10}(x_q)}$ is the median of the twelve months of precipitation for year *p*, and *n* is the number of years of data for station *r*.

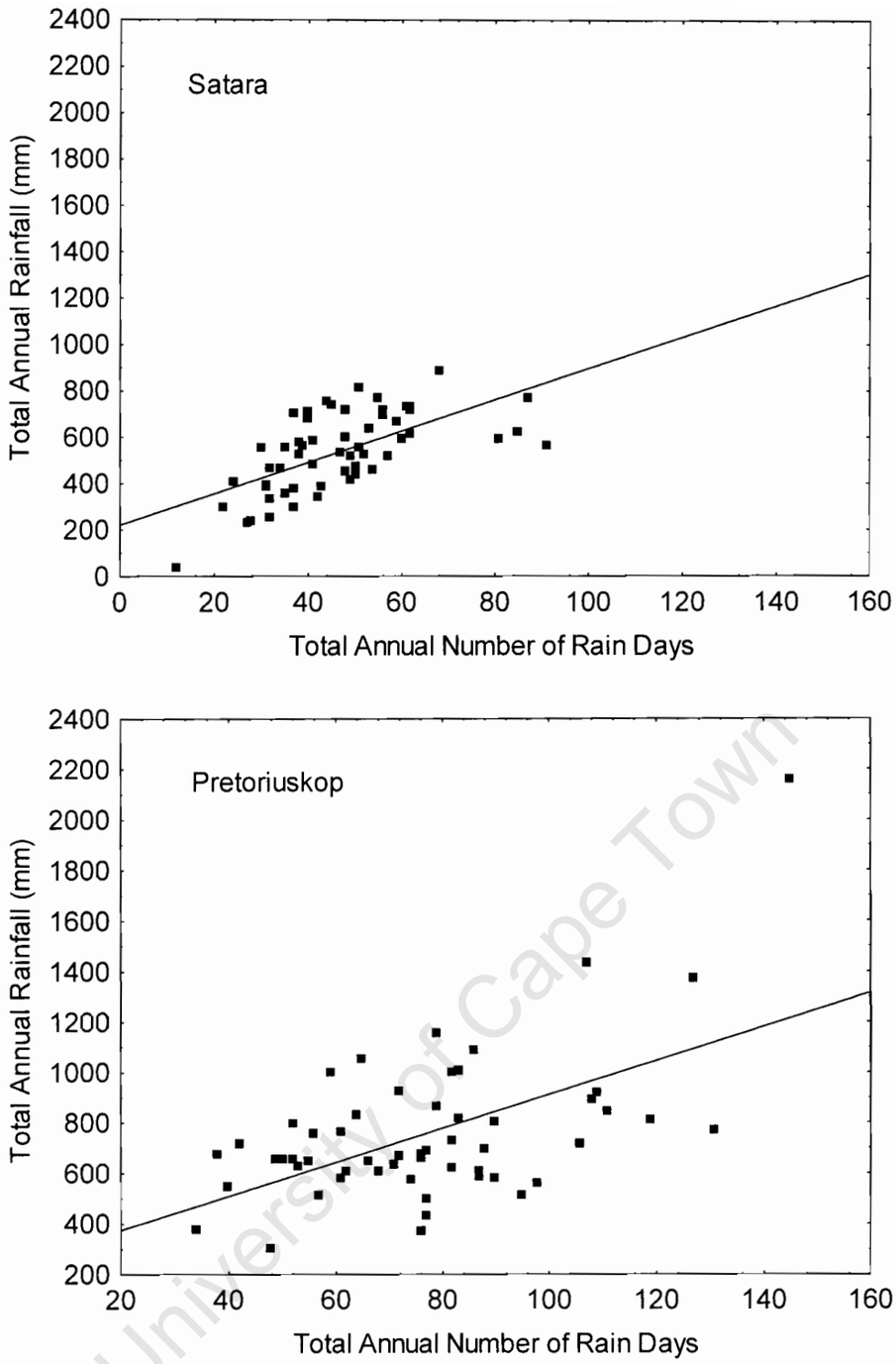

Figure 1 The correlation between total number of rain days and total precipitation (mm) for Pretoriuskop ($R^2 = 0.31$, $p < 0.000$, $F_{1, 56} = 23.45$) and Satara ($R^2 = 0.39$, $p < 0.000$, $F_{1, 56} = 34.87$) for a total of 57 years with no missing records starting from 1933 to 2002.

Results

(i) Is rainfall variability higher at Satara than Pretoriuskop?

Although annual rainfall is significantly different between the two sites, there was no significant difference in the annual yearly variation in rainfall (AYV) between Satara (mean = 0.03) and Pretoriuskop (mean = 0.02) (t-test: $t_{1, 111} = 1.56$, $p = 0.121$, F-ratio = 1.13). The average yearly rainfall for Pretoriuskop (average = 734 mm, st. dev. = ± 296 mm) is significantly higher than that of Satara (average = 546 mm, st. dev. = ± 160 mm) (t-test: $t_{1, 111} = 4.40$, $p < 0.000$, F-ratio = 3.41). The calculated annual coefficient of variation (CV) of precipitation is 40 % for Pretoriuskop and for Satara 29 %. The year 1939 represents an outlier for Pretoriuskop and removing this point reduces the coefficient of variation for Pretoriuskop from 40 % to 32 %.

(ii) Is there a relationship between the number of rain days and annual rainfall?

There was a significant linear relationship between total number of rain days per year and total annual rainfall (Fig. 1) for Pretoriuskop ($R^2 = 0.31$, $p < 0.000$, $F_{1, 56} = 23.45$) and Satara ($R^2 = 0.39$, $p < 0.000$, $F_{1, 56} = 34.87$). Although Satara had less total annual rainfall and number of rain days per year, the slope of the relationship between number of rain days and total annual rainfall was near equal to that of Pretoriuskop (Satara: $y = 6.72x + 239.27$; Pretoriuskop: $y = 6.76x + 220.18$).

Although Satara has fewer rain days than Pretoriuskop, Pretoriuskop experienced slightly longer dry spells within the rainy season compared to Satara. Dry spells within the rainy season are common for both Satara and Pretoriuskop (Fig. 2). Sequences of 4 dry days or less accounted for 48 % of the total dry days (excluding the dry season months) for Pretoriuskop and 43 % for Satara (Fig. 2). Twenty eight consecutive dry days or less accounted for 91 % of the total consecutive dry days for Pretoriuskop compared to twenty one days for Satara (Fig. 2). The longest dry spell,

when the start of the rain season is taken to be the 01 of August was 255 consecutive days for Satara and 225 for Pretoriuskop.

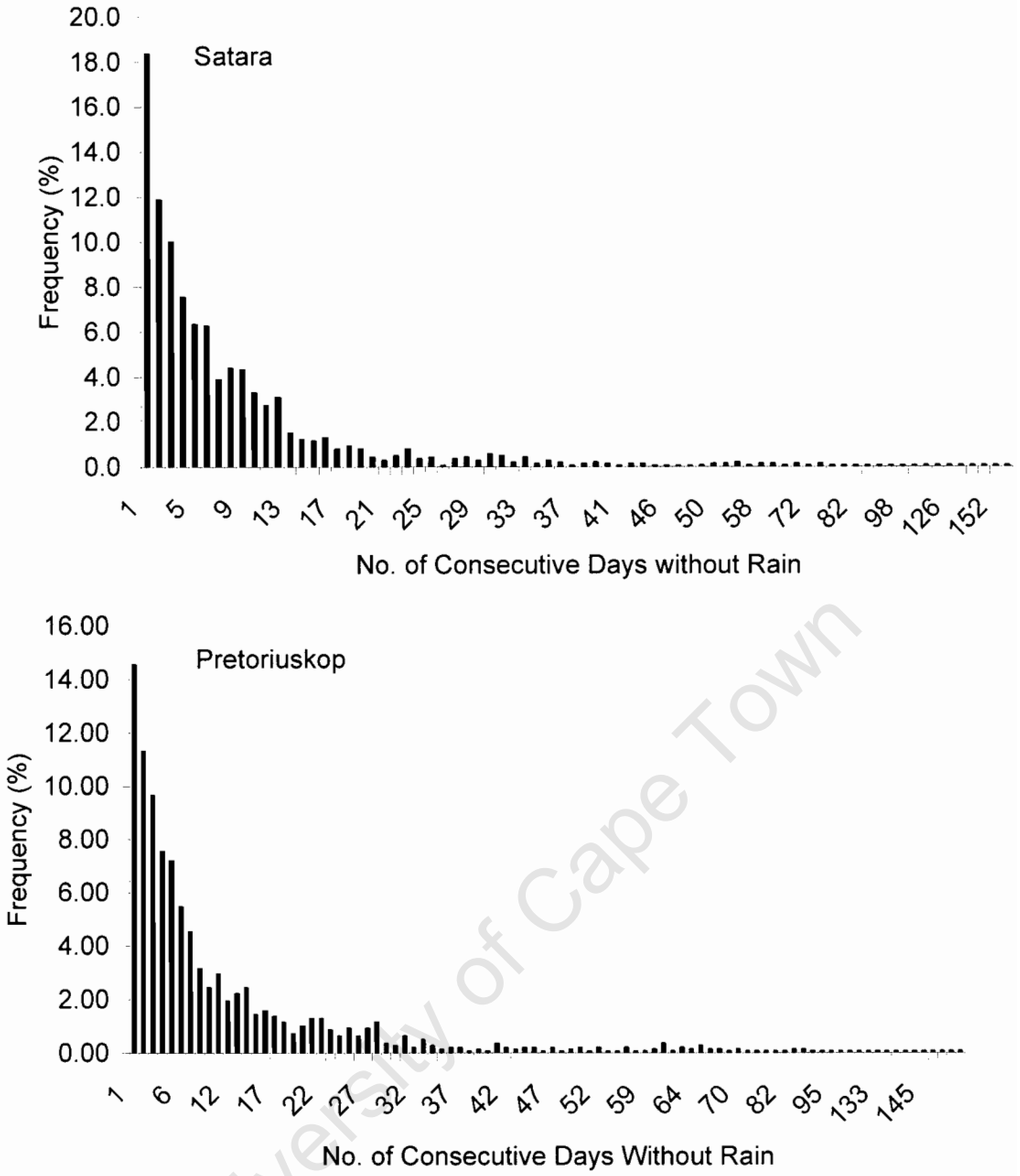

Figure 2 The frequency of consecutive number of days without rain during the months of September to April for Pretoriuskop and Satara for a total of 57 years with no missing records starting from 1933 to 2002.

(iii) Does Pretoriuskop have a longer wet season compared to Satara?

There was no difference between Pretoriuskop and Satara when the length of the rainy season was defined as the period where the probability of receiving a 10-day dry spell is less than 0.5 (Cook & Heerdegen, 2001) (Fig. 3). By this definition the length of the rainy season is approximately 200 days long for both Satara and Pretoriuskop from the end of September to the end of March (Fig. 3). Cook & Heerdegen (2001) further defined a wet season within the rainy season as a period where the probability of a 10-day dry spell is less than 0.1. This enabled them to identify the period in the year when the monsoon weather was at its peak. Similarly the rainfall for Satara and Pretoriuskop was highly concentrated (Fig. 4), yet no period exists where the probability of a 10-day dry spell is less than 0.1 (Fig. 3).

Pretoriuskop had a higher probability of 30 consecutive no-rain days within the rainy season despite more than 50 % of Satara's rainfall being concentrated in three months compared to four for Pretoriuskop (Fig. 4). Satara received approximately 200 mm less rain a year and had a three month longer dry period (where the average monthly rainfall is lower than 40 mm) compared to Pretoriuskop (Fig. 4), yet only had a period of 53 days at the peak of the dry season where there is a > 40 % chance of receiving an extended dry spell. In contrast, Pretoriuskop had a period of 95 days from the end of April to the start of August with a higher than 40 % probability of experiencing a 30-day dry spell (Fig. 3). The 50 % chance of both sites experiencing a 30-day dry spell occurred for a much smaller period in the middle of the year compared to that of a 10-day dry spell (Fig. 3b). More than 80 % of the years for both sites had experienced at least one 30-day dry spell within the months from September to April.

Average monthly rainfall was distinctly seasonal for both sites (Fig. 4). The monthly distribution of rainfall suggests that Pretoriuskop had a slightly earlier start to the rainy season compared to Satara. For Pretoriuskop, approximately 56 % of the total precipitation occurred within only four months of the year (between November and February), whereas 50 % of Satara's rainfall occurred within three months of the year (from December to January).

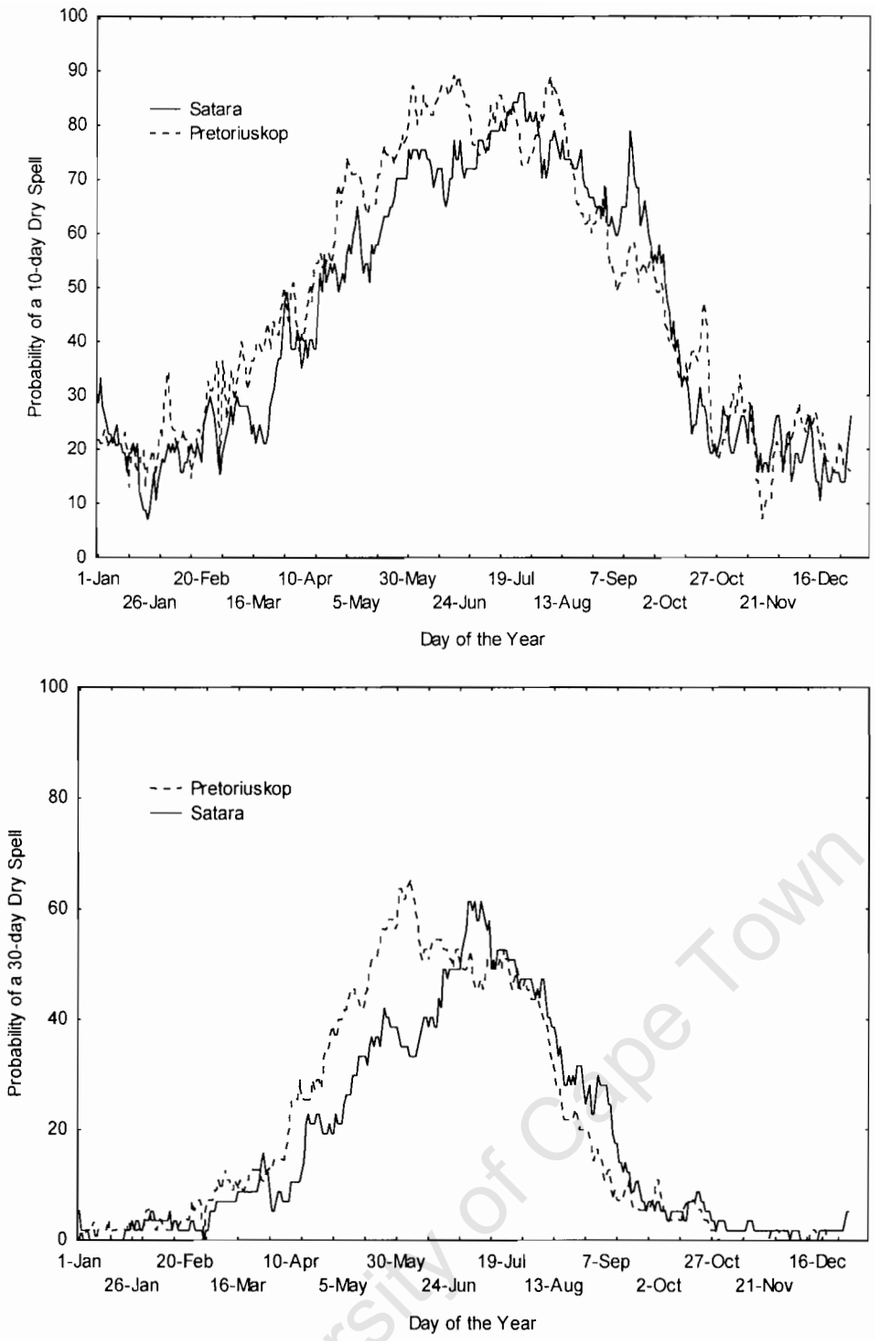

Figure 3 The probability of a 10- or 30- day dry spell occurring on every day of the year for Pretoriuskop and Satara for a total of 57 years with no missing records starting from 1933 to 2002.

Seven of the Satara months have rainfall below 40 mm (April to October) compared to five for Pretoriuskop (May to September) (Fig. 4). The biggest difference in average rainfall between months occurred between September and October (difference of 38 mm) for Pretoriuskop and between October and November (difference of 39 mm) for Satara (Fig. 4). As indicated by the AMV values, monthly

rainfall averages were more variable between the months of May to August for Pretoriuskop and between May to September for Satara (Fig. 4).

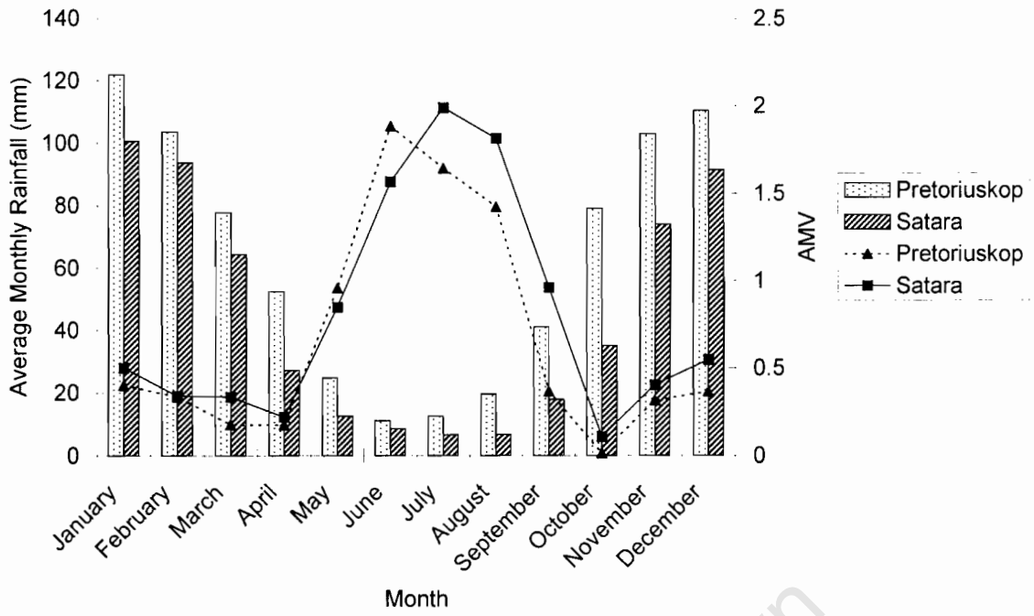

Figure 4 The mean monthly precipitation (mm) (bars) and among month variation (AMV) (lines) for Pretoriuskop and Satara for a total of 57 years with no missing records starting from 1933 to 2002.

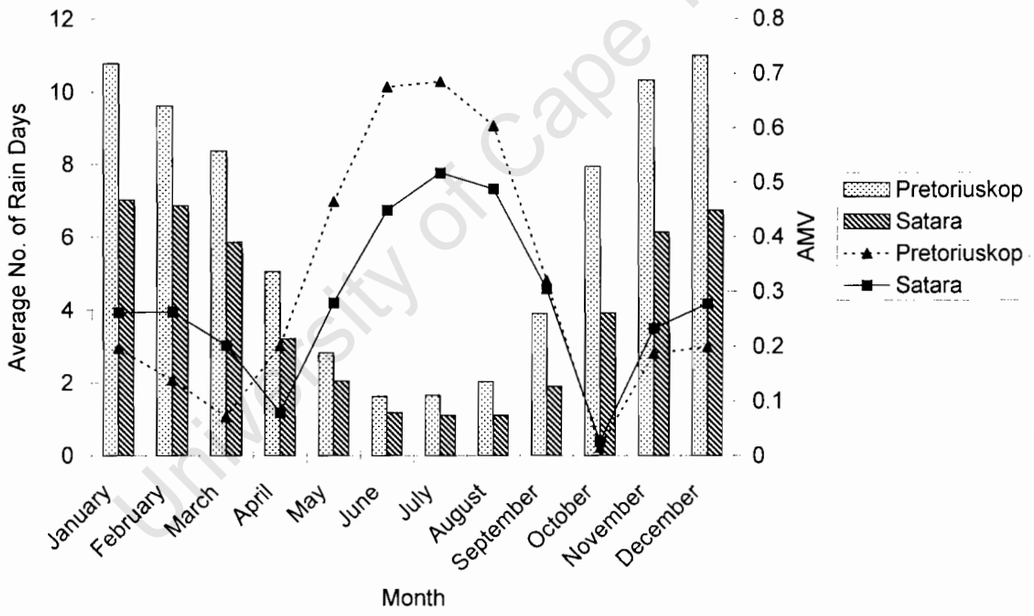

Figure 5 The mean number of rain days (> 5mm) (bars) and among month variation (AMV) (lines) per month for Pretoriuskop and Satara for a total of 57 years with no missing records starting from 1933 to 2002.

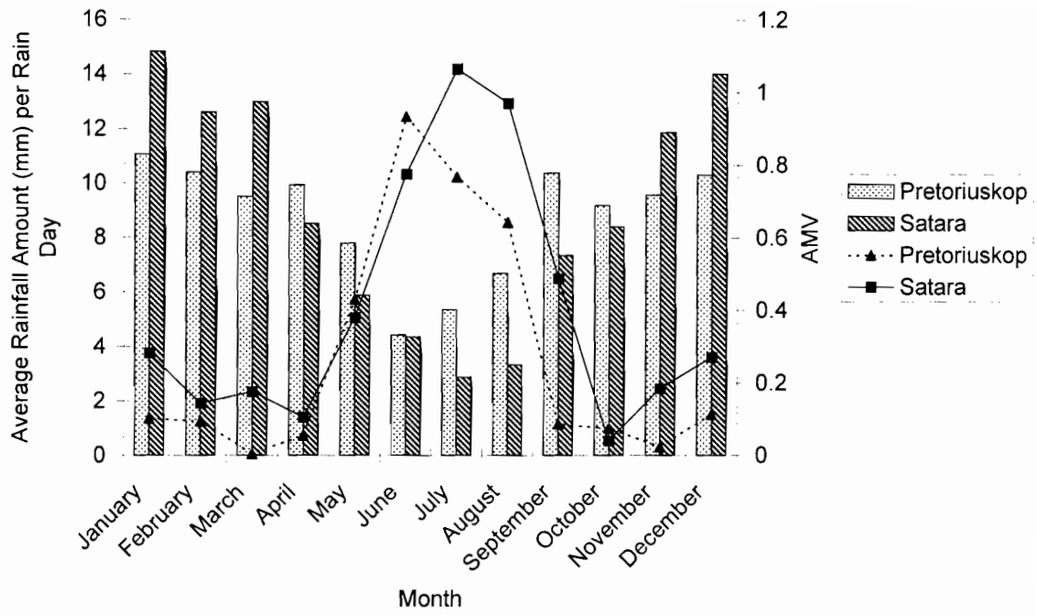

Figure 6 The average precipitation (mm) amount per rain day and among month variation (AMV) (lines) for Pretoriuskop and Satara for a total of 57 years with no missing records starting from 1933 to 2002.

Mean daily rainfall amount (mm) was calculated by dividing the monthly rainfall totals by the total number of rain days in a month (Fig. 5) and obtaining an average over the 57 rainfall years. Both sites had higher variability in the average daily rainfall amount and average number of rain days during the drier months (Fig. 5 and 6). Mean daily rainfall amount for Pretoriuskop ranged from a maximum of approximately 11 mm in January to approximately 4 mm in June (Fig. 6). In contrast, Satara had a more distinct change in mean daily rainfall amount from the wet season (approximately 15 mm in January) to the dry season (3 mm in July). From the range of AMV values across Figure 3 – 6, mean monthly rainfall was the most variable for both sites (Fig. 3) followed by mean rainfall amount per rain day (Fig. 6) and average number of rain days (Fig. 5).

(iv) Is there a higher frequency of the right rainfall conditions for germination and survival occurring at Pretoriuskop compared to Satara?

There was a smaller chance of receiving big rainfall days compared to small rainfall days for both Satara (Fig. 7a) and Pretoriuskop (Fig. 8a). Figure 7a and 8a depict the amount of times over the last 57 years that Pretoriuskop and Satara had encountered

days of different rainfall amounts (>10 mm, > 25 mm, > 50 mm, > 75 mm, > 100 mm) across the rainy season months. For these graphs (Fig. 7a and 8a), the second constraint was kept constant (a total of 30 mm within 30 days) and thus only the probability of a given day receiving rainfall of different sizes was calculated.

There was between 50-60 % less chance of follow-up rain within a certain amount of time following a big rainfall day (> 50 mm) than a 10 mm rainfall day (Fig. 7b-e, 8b-e). This would suggest that enough rainfall to stimulate a large germination event and enough subsequent rain to ensure survival was rarely met (Fig. 7c and 8c). In contrast to germination after a large rainfall event, germination after a small rainfall event had a higher probability of receiving follow-up rain (Fig. 7b, c and 8b, c).

Rainfall combinations that are conducive for seedling establishment occurred during the peak of the rainy season for Satara whereas for Pretoriuskop the start towards the middle of the rainy season had suitable conditions (Fig. 7b, d and 8b, d). Follow-up rain within a given time after a small rainfall day had almost equal chance of occurring from September through to December for Pretoriuskop (Fig. 8b, d) and then declines after December. For Satara, the first rainy season months were as variable as the end of the rainy season (Fig. 7b, d). The highest likelihood of a large rainfall event to stimulate germination followed by sufficient rain to ensure survival occurred slightly later during the rainy season (January-February) for Satara (Fig. 8c) than Pretoriuskop (Fig. 9c).

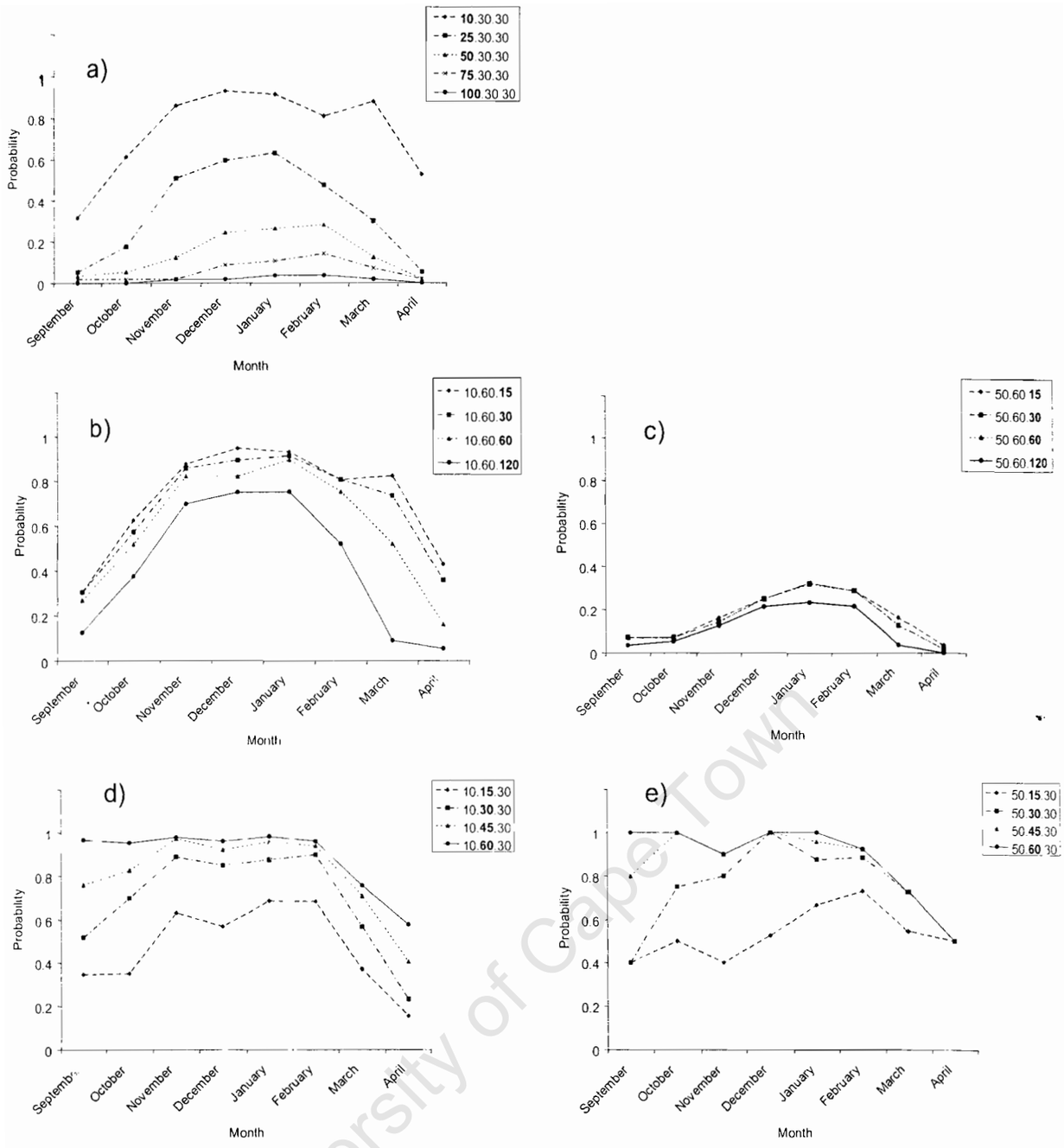

Figure 7 The probability of receiving different rainfall combinations for Satara. The first number in a series of three (10.15.30) refers to the first rainfall amount (10 mm), followed by 30 mm within 15 days. **a)** the probability of receiving a rainfall day with more than 10, 25, 50, 75 and a 100 mm of rain with a total of 30 mm within the next 30 days. **b-c)** probability of receiving 15, 30, 60 and 120 mm of rainfall within 60 days of a 10 mm (b) and a 50 mm (c) rainfall day. **d-e)** probability of receiving 30 mm of rain within 15, 30, 45 and 60 days of a 10 mm (d) and 50 mm (e) rainfall day.

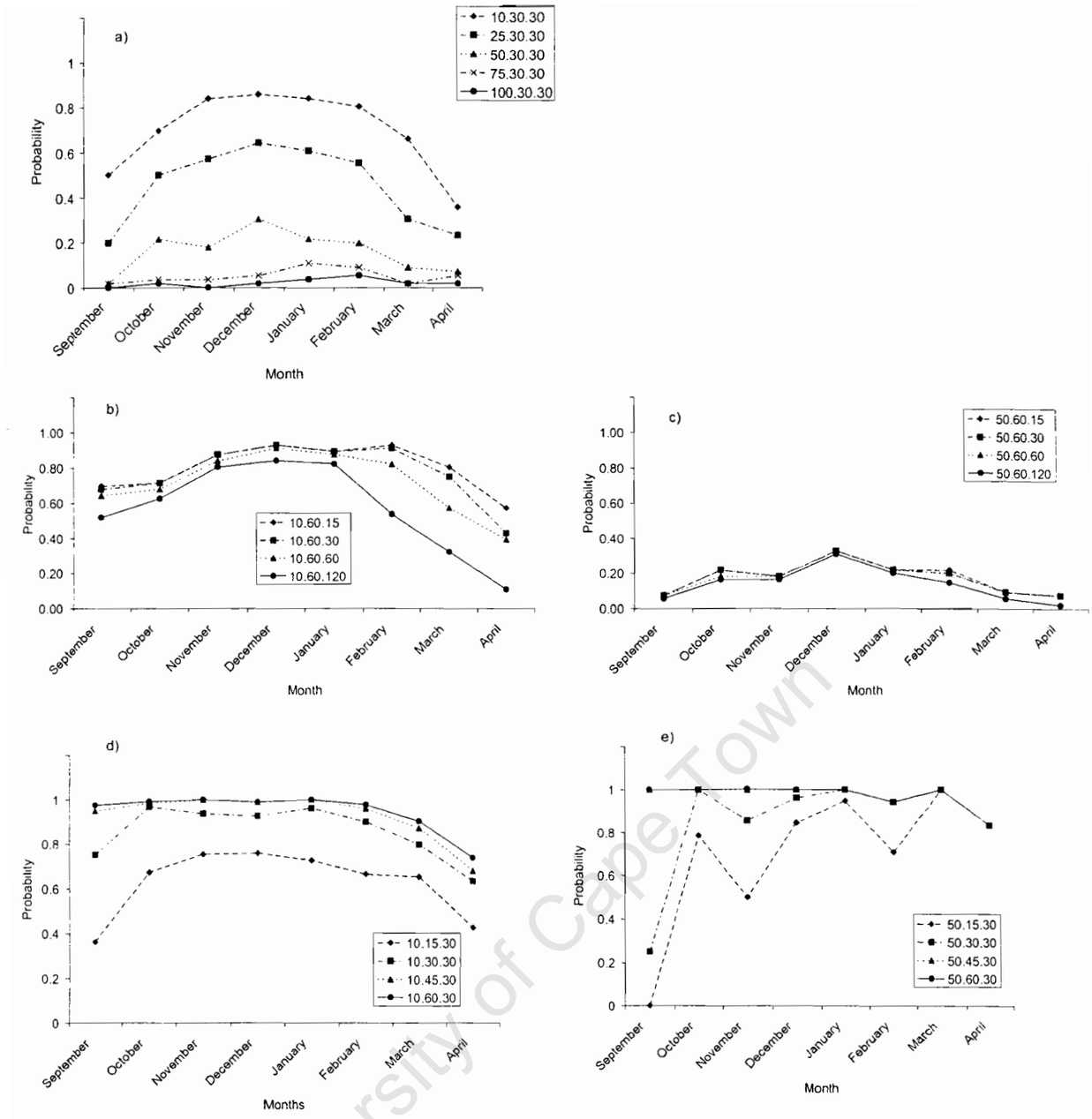

Figure 8 The probability of receiving different rainfall combinations for Pretoriuskop. The first number in a series of three (10.15.30) refers to the first rainfall amount (10 mm), followed by 30 mm within 15 days. **a)** the probability of receiving a rainfall day with more than 10, 25, 50, 75 and a 100 mm of rain with a total of 30 mm within the next 30 days. **b-c)** probability of receiving 15, 30, 60 and 120 mm of rainfall within 60 days of a 10 mm (b) and a 50 mm (c) rainfall day. **d-e)** probability of receiving 30 mm of rain within 15, 30, 45 and 60 days of a 10 mm (d) and 50 mm (e) rainfall day.

There was more than an 80% chance that both Satara and Pretoriuskop will receive 30 mm of rain within 30, 45 or 60 days after a 10 mm rainfall day (Fig. 7 d and 8 d). Figure 7 (d and e) and 8 (d and e) depict the probability of a month receiving a sum of 30 mm of rain within varying amount of days (15, 30, 45 and 60 days) following a 10 mm and 50 mm rainfall day. Only the smallest rainfall combination (30 mm in 15 days after a 10 mm rainfall day) had a below 80% chance of occurring in any given month for both sites. Again apart from the largest rainfall combination (30 mm of rain within 60 days) chances of receiving 30 mm of rain within 15, 30 and 45 days after a 10 mm rainfall day had a distinct unimodal distribution for Satara (Fig. 8d). For Pretoriuskop, the probability of these rainfall "combinations" occurring after a 10 mm rainfall day only flattened off for the first (September) and last (April) months of the wet season (Fig. 9d).

The chances of Pretoriuskop receiving 30 mm of rain within 15 or 30 days after a 50 mm rainfall day were very small for September (Fig. 9e) and then improved for the remainder of the months. For Satara, the highest probability of receiving 30 mm of rain within 30-60 days after a 50 mm rainfall day, was in December (approximately 100% chance) and then declined towards April (40%).

Discussion

This study supports the idea that rainfall variability is site specific (Davidowitz, 2002) and not just a general function of annual rainfall (Higgins *et al.,* 2000). The overlap in rainfall variability between Satara and Pretoriuskop may be partially due to the close geographic proximity between the two sites and hence shared weather systems (Venter & Gertenbach, 1986). Anti-cyclonic systems move semi-rhythmically from west to east and influence the weather systems of the entire sub-continent (Venter & Gertenbach, 1986).The establishment of equatorial low-pressure troughs over the subcontinent normally results in widespread and continuous rain across the Lowveld (Venter & Gertenbach, 1986).

This suggests that another factor apart from the effects of rainfall variability on seedling recruitment is required to explain the co-existence of trees and grasses at the

semi-arid Satara site (Higgins *et al.,* 2000). Even though vegetation biomass is greater at Pretoriuskop than Satara, the high nutrient basalt soils of Satara support a higher herbivore biomass. The effect of browsing is ignored by the Higgins *et al.,* (2000) model but may be significant in limiting tree seedling establishment. In an east African savanna establishment of *Acacia karoo* was correlated to epidemic outbreaks of rinderpest that caused large mortality of impala (Prins & van der Jeugd, 1993).

Unlike the tropical savannas of Australia none of the two sites had a wet period in the rainy season where the probability of a 10-day rain spell was less than 0.1 (Cook & Heerdegen, 2001). Similarly for the Masai Ecosystem of northern Tanzania the variability of rainfall was lowest during the period of monsoon rains (Prins & Loth, 1988) which suggests that tropical savannas with a monsoon influence have less variable rainfall. Conversely the length of the wet season was found to decrease with annual rainfall in the study of Cook & Heerdegen (2001) but not for Satara and Pretoriuskop. In Cook & Heerdegen's (2001) study, Larrimah a station with similar rainfall to Pretoriuskop (806 mm) has a rainy season with a duration of 144 days compared to 200 for Pretoriuskop, whereas Elliot (517 mm) with a rainfall similar to that of Satara has on average a 119 day long rainy season compared to 200 for Satara. Similarly essentially one rainy season was defined for the Masai Ecosystem in northern Tanzania across a rainfall gradient from 434 mm to 1003 mm (Prins & Loth, 1988).

The seedling's perspective

Unlike the predictions that seeds should germinate with the first rains, the results here suggest that a large rainfall event with subsequent follow-up rain is more probable for the mid rainy months of Pretoriuskop and late rainy months of Satara. Germination after a small rainfall event with follow-up rain is also most probable during the mid rainy months for Satara but for Pretoriuskop the beginning to mid rainy months is favourable. The slightly sooner start to the wet season at Pretoriuskop is the only indication that seedling establishment success could be higher at Pretoriuskop if germination earlier in the rainy season equates to reduced mortality in the subsequent dry season (Jordan & Nobel, 1979).

Predictions

The more frequent but smaller daily rainfall events of Pretoriuskop compared with Satara, combined with the differences in water holding capacity of the soil substrate between the two sites, may also affect rooting distribution of grasses and trees. Deep-rooting species should be favoured at Satara whereas shallow-rooting trees should be more successful at Pretoriuskop. Given that rainfall conditions conducive for seedling establishment are equally probable at both sites, it is interesting that Satara has lower tree densities compared to Pretoriuskop. This suggests either that other factors are limiting seedling recruitment at Satara, or that the recruitment stage is not the critical demographic bottleneck limiting tree cover. Increased mammal herbivory may significantly reduce seed availability through the consumption of flowers and seed (Coe & Coe, 1987; Miller, 1995) and reduce seedling survival (Prins & van der Jeugd, 1993) at Satara compared to Pretoriuskop. Tree toppling by elephants of *Acacia nigrescens,* the dominant species at Satara is also common and the dehiscent seeds of this species are poor at surviving fracturing by the molar teeth of herbivores (Coe & Coe, 1987).

Alternatively, not the recruitment stage but sapling escape could be the most important factor limiting tree density. Yearly background recruitment may occur but established seedlings (saplings) are heavily browsed or burnt too frequently to grow into trees.

Conclusion

This study presents an analysis on rainfall variability; length of the wet season and conditions conducive to seedling establishment, *i.e.* a thorough investigation of rainfall variability and what it suggests about plant phenology with timing of seedling establishment. Rainfall variability is comparable for Satara and Pretoriuskop and appears to be related to site condition and shared weather systems and not annual rainfall. Thus a mechanism other than increased rainfall variability influencing recruitment is required to explain the co-existence of trees and grasses at the semi-arid Satara site. In another savanna, the Masai Ecosystem of northern Tanzania (Prins & Loth, 1988), mean annual rainfall was also found to be unrelated to coefficient of variation (CV) of annual rainfall. In this study mean monthly CV was correlated to

annual rainfall and considered a better index of uncertainty. Enlarging the sample sites to include a larger rainfall gradient and geographic areas influenced by different weather systems should reveal the importance for rainfall variability as opposed to other mechanisms such as herbivory. The analysis reveals that the peak rainy months and not the start of the wet season are most conducive to germination and seedling survival for Satara and Pretoriuskop. Germination after the first large rainfall event, which is most probable during the peak rainy months, would maximise early establishment which may influence dry season survival (Jordan and Nobel, 1979).

Go to the glass house and observe the seeds. Nothing has sprouted in three days and this is causing you to worry. You want to start digging around to see if you actually planted them but this might unbalance the delicate balance.

- *A. Botha (*Behaving organically - Benediction Magazine).

Chapter 4

The influence of wet season length on dry season tree seedling survival

Abstract

I tested whether the length of the wet season influences dry season survival for two savanna species, *Philenoptera violacea* and *Acacia nigrescens* by growing seedlings at a field site in the Kruger National Park. Seedlings were established under two irrigation regimes, that of a below-average and above-average Satara rainfall year. Rainfall was controlled by the erection of rain-out shelters. There was no difference in dry season seedling survival for seedlings of both species that received a two-month below-average rainfall year and those that received a four month above-average rainfall year despite significant differences in seedling size. Highest mortality immediately after germination despite of irrigation suggests that surviving dry spells within the wet season are more critical for successful seedling establishment. The absence of a seed bank implies that bet-hedging to straddle unsuccessful germination events are not a common strategy for savanna tree species in the Kruger National Park. No natural germination was recorded in the field at Satara, which suggests that the absence of seed may limit tree seedling establishment opportunities.

Introduction

Savannas are characterized by having highly variable rainfall regimes (Adiku, 1997; Prins & Loth, 1988; Sala *et al.*, 1992). Unpredictability in the timing and distribution of rainfall within the rainy season can limit seedling establishment. Seeds should therefore germinate at the start of the rainy season (Khurana & Singh, 2001; Williams, 1999) to increase the chances of dry season survival. Early germination would allow seedlings the opportunity to maximise the length of the rainy season to grow root reserves. However lack of follow-up rain after a germination event would cause seedling mortality (Hoffman, 1996; Keya, 1997).

The hypothesis that seeds should germinate with the first rains to maximise the wet season growth period does not consider the risk of dry periods following germination. This risk is not equal across the rainy season months (Prins & Loth, 1988). For example in the Masai ecosystem of northern Tanzania the most predictable rain occurred at the end of the rainy season and hence seed-set and growth is considered more certain during these months (Prins & Loth, 1988). However seedlings that establish late in the wet season may have poor dry season survival if seedlings do not have enough time to grow sufficient root reserves (Jordan & Nobel, 1979). Seedling survival may thus be a trade-off between enough time to grow sufficient resources to survive the dry season and germinating at a time in the rainy season when there is a high probability of receiving follow-up rain (Barnes, 2001; Clauss & Venable, 2000). Areas that have more favorable conditions for seedling germination and survival early in the rainy season compared to later in the rainy season may thus have more frequent establishment events (Chapter 3).

Spreading the risk of germination over several rainfall events is one way of overcoming within rainy season variability (Clauss & Venable, 2000). For some dessert annuals only a proportion of the seed bank germinates in a given year or rainfall event (Clauss & Venable, 2000). Spreading the risk of germination in such a manner, known as bet-hedging, increases the chance of at least one germination episode resulting in seedling survival and seed set (Clauss & Venable, 2000).

However unlike desert annuals, seed banks of species of dry tropical ecosystems are often small (Skoglund, 1992) or almost non-existing (Witkowski & Garner, 2000). In their study Witkowski & Garner (2000) found that seed bank densities were less than 5 seeds / m^2 in the soil beyond the edge of the adult tree canopy for *Acacia nilotica, Acacia tortilis* and *Dichrostachys cinerea*. These species have a predominantly transient seed bank since most of the seed found across all micro sites (including underneath the tree canopy) were in the litter layer as opposed to the soil (Witkowski & Garner, 2000). Annual species that have only one opportunity to produce seed increase their fitness by spreading the risk of germination over several episodes. In contrast, long-lived savanna trees can afford to risk germinating nearly all their seeds in one year since the adults persist to produce seed in the following year if a germination event is unsuccessful. For example, in Australia Zammit & Westoby (1987) found risk spreading (more gradual seed release and germination) for the obligate seeder *Banksia ericifolia* than the resprouter *Banksia oblongifolia.*

Rainfall variability can be overcome not only through optimal timing of germination of the seeds but also through drought adaptations of the seedlings. Very little is known about the ecophysiological characteristics of tree seedlings relative to stress resistance (Medina & Silva, 1990). Physiological adaptations for postponing drought may include deep, dense rooting systems, high root: shoot ratios (Choinski & Tuohy, 1991; Otieno *et al.*, 2001), stomatal closure and/or leaf shedding to reduce transpiration or stomatal opening and/or leaf orientation away from direct sun to reduce high leaf temperatures.

In this chapter I determine how dry season tree seedling survival is influenced by different lengths of time to grow in the preceding rainy season. I also determine how the timing of germination differs between two sites with different rainfall totals and lastly I investigate the presence of persistent seed banks from experimentally excavated seed banks. Specifically I ask (i) does the length of growth during the rainy season influence dry season survival, (ii) when do tree species germinate, (iii) what are the physiological adaptations to drought stress and (iv) do savanna tree species form seed banks?

To determine how the length of growth influences dry season survival I grew seedlings at two sites with different soil types (Chapter 2) in the Kruger National Park for different periods during the rainy season before withholding water and recorded the length of the no-rain period they were able to survive. To determine when tree species germinate, I conducted monthly surveys for newly emerged seedlings in two areas with different annual rainfall in the Kruger National Park. I also planted seeds of various species monthly from September 2003 to December 2003, and applied a simulated 60 mm rainfall event and recorded germination. To determine physiological adaptations to drought stress I recorded leaf temperature and transpiration rates for seedlings of two species and leaf shedding of six species over a period of increased drought stress. To determine which savannas tree species form a seed bank I excavated soil samples at two sites and recorded the presence of seed.

Methods

(i) Does the length of growth during the rainy season influence dry season survival?

I planted seeds of ten species at two field sites in the Kruger National Park and rainfall events were supplemented with irrigation after germination.

Field sites

Two 15 m by 15 m sites were fenced off inside the Pretoriuskop (granite sand) and Lower Sabie (basalt clay) tourist camps. Both sites were cleaned of all grass by scraping with a spade along the top 5-10 cm surface of the soil and using a pick for deeper-rooted plants. Grass was removed throughout the experiment when necessary. I assigned one species to a row that was approximately 13.5 m long spaced 1.5 m apart on the sand and 1.75 m apart on the clay. For all species, the respective rows were divided into five treatments that were spaced 1.5 m apart on the sand and 1.75 m on the clay. I marked out 36 spots in each treatment using nails with washers attached,

being 25 cm apart longitudinally and 25 cm apart across. I left a gap of 50 cm was left between rows to allow space for the irrigation piping.

Species and treatment of seeds

Subject to seed availability the dominant species at Pretoriuskop (*Terminalia sericea*) and Satara (*Acacia nigrescens)* were chosen for the field experiment. *Colophospermum mopane* and *Adansonia digitata* were included but occur further north on basalt clay and granite sand respectively. *Sclerocarya birrea, Combretum apiculatum, Combretum hereroense, Terminalia sericea* and *Adansonia digitata* were selected for planting at the Pretoriuskop site and *Acacia nilotica, Cassia abbreviata, Philenoptera violacea, Colophospermum mopane* and *Acacia nigrescens* for the Lower Sabie site. Seeds were collected from two to three healthy-looking adults in the months prior to the start of the experiment (September 2002). Seeds were stored in paper bags in a cool, dark environment. I removed the coats of *Combretum hereroense, Combretum apiculatum, Colophospermum mopane, Philenoptera violacea* and *Pterocarpus angolensis* with a pair of scissors. For *Terminalia sericea* the seed coat was clipped away on all sides but not removed. The seeds of *Adansonia digitata* were removed from the fruits using a small jigsaw. I left seeds of *Acacia nilotica* in hot water overnight prior to planting. I lightly scraped the seed tip of *Cassia abbreviata* using sandpaper.

Approximately 1000 seeds per species (except for *Sclerocarya birrea* and *Cassia abbreviata* where fewer seeds were available) were planted on the 1st of November at Pretoriuskop and the 3rd of November at Lower Sabie after the first rains of the wet season (Fig. 1, first dotted line). Both sites received rain immediately after planting.
I recorded emergence, death, number of leaves, or leaflets for *Acacia nigrescens*, and height of seedlings at regular intervals.

Irrigation

Irrigation after germination was done to reduce mortality within the rainy season (Fig.1). I followed no set-watering schedule and irrigated during times of no rain when seedlings started to wilt (Fig. 1). Where possible, I applied water on cloudy

days or very early/late in the day to reduce evaporation losses. The irrigation system comprised a 15 mm diameter standard black irrigation piping with micro jet sprays inserted every 1.2 m. I positioned the nozzles to allow application of water in an even fashion, so water from two adjacent sprays just overlapped. To estimate the total amount of water received by each species an inline flow meter was attached to the system to monitor the applied amount of water. The total time of irrigation and water meter readings was recorded. There was a positive relationship between total time of irrigation and total litres per irrigation event for Lower Sabie ($R^2 = 0.66$, $p = 0.00$) and for Pretoriuskop ($R^2 = 0.96$, $p = 0.00$) which was used to convert irrigation events to rainfall events (l/m^2).

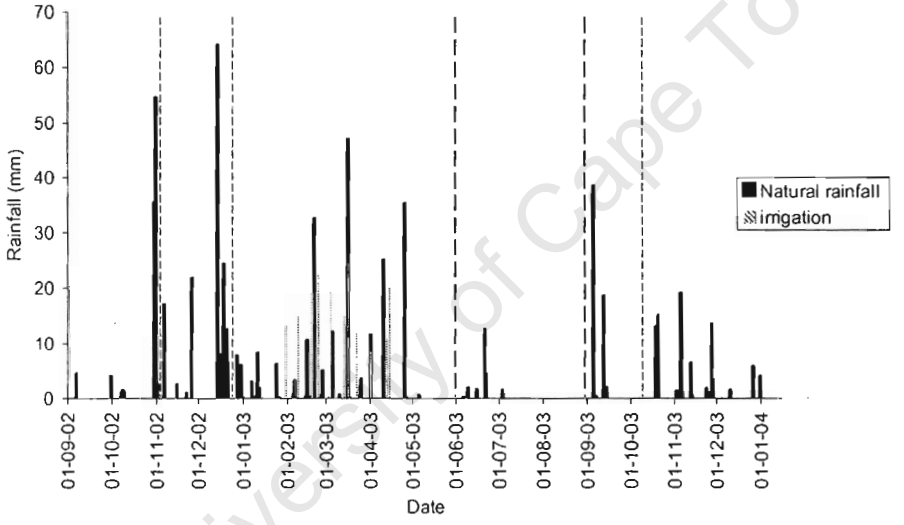

Figure 1 The natural rainfall and irrigation events for Lower Sabie from September 2002 to the end of May 2003. The first dotted line indicates the time of planting for all species at Lower Sabie, the second and third line indicates the time at which all *Acacia nigrescens* and *Philenoptera violacea* seedlings had dropped their leaves respectively. The fourth line indicates the time at which seedlings of *Philenoptera violacea* and *Acacia nigrescens* seedlings outside of the rain-out shelters started resprouting new leaves.

Soil Moisture

To determine the soil moisture at which seedlings displayed stress and to test how differences in the lengths of the rainy season influenced soil moisture I measured volumetric soil moisture content. I augured holes to bedrock in the middle of selected

treatments using a soil auger and inserted permanent plastic sleeves. I measured soil moisture by inserting a moisture probe (Sentek Diviner 2000 capacitance probe) into the pipes at regular intervals. An independent study showed that the measurement precision of the Diviner probe was better than 0.01 m^3 m^{-3} (Evett *et al.*, 2003).

Manipulation of the length of the rainy season

Germination was low and only the two species with the highest germination, *Philenoptera violacea* and *Acacia nigrescens* on the basalt clay were used to test the influence of the length of the rainy season on dry season survival. For these two species there were significant differences in soil moisture between plots separated by a few meters and therefore I reduced the number of treatments to the following: a) Long-moist rainy season: Four-month rainy season with volumetric soil moisture of the deepest layer > 42 %, b) Long-dry rainy season: Four-month rainy season with volumetric soil moisture < 42 % of the deepest soil layer and c) Short rainy season: Two-month rainy season with volumetric soil moisture < 33 % of the deepest layer (Table 1).

To reduce the length of the rainy season for the short rainy season treatments (c) I erected rain-out shelters on one plot of *A. nigrescens* and one plot of *Philenoptera violaceae*. Plots were chosen based on number of seedlings to make statistical comparison between rainout and other treatments possible. The rain-out treatments received rainfall and irrigation water for approximately two months after maximum germination until I erected the roofs. The rain-out treatments received water to the equivalent of a below-average Satara rainfall year (25% quartile = 436 mm) (*Philenoptera violacea* = 446 mm (rainfall: 362 mm; irrigation: 84mm); *Acacia nigrescens* = 451 mm (rainfall: 362 mm; irrigation: 89 mm)). The remaining treatments received the equivalent of an above-average Satara rainfall year (75% quartile = 692 mm). *Philenoptera violacea* treatments received 756 mm and the *Acacia nigrescens* treatments 727 mm of rain and irrigation water for approximately four months after maximum germination.

Table 1 Watering treatments at Lower Sabie (basalt clays). The plots of *Acacia nigrescens* and *Philenoptera violacea* were divided into three treatments according to volumetric soil water content (%). The deepest layer for the four-month rainy season treatment of *Philenoptera violacea* was significantly wetter (H (5, 102), = 30.95, p < 0.000) than the rest of the treatments (as indicated by the superscript letters).

	Acacia nigrescens			*Philenoptera violacea*		
Treatment	**Mean Volumetric Soil Moisture (%)**	**N**	**St. Dev**	**Mean Volumetric Soil Moisture (%)**	**N**	**St. Dev**
Four-months wet season deepest layer > 42 %	41.74^{B}	18	11.83	56.85^{A}	18	13.55
Four-month wet season deepest layer < 42 %	35.53^{B}	15	8.75	40.60^{B}	21	15.20
Two-month wet season deepest layer < 33 %	31.92^{B}	17	6.64	32.73^{B}	13	5.06

The rainout exclosures extended approximately one meter on all sides of the treatment and was designed to stand on four corner metal poles that were buried approximately one meter into the ground. The exclosures had an A-shape roof that was approximately 2 m high at the apex with gutter attached all around the base that stands approximately 1.5 above the ground. The roof is slightly raised on one side to allow rainwater to drain freely from the outlet hole through the outlet pipe that leads water away from the site. The roof material consisted of transparent plastic sheeting that could be rolled up to prevent shading on no-rain days. When no one was available to secure the sheeting before a rainfall event the sheeting was kept down. Soil volumetric measurements of the plots showed that the soil moisture of the rainout shelters reduced from the time they were erected and were not influenced by lateral movement of water from rainfall events (Fig. 3).

Statistical Analysis

I used a simple one way ANOVA to test for mean differences in seedling size and mean age at death between treatments. In the case where the assumption of equal variances was violated I used a Kruskal-Wallis test. A Tukey Honest Significant Difference post-hoc test was used and, in the case of non-equal variances, the non-parametric Multiple Comparisons of Mean Ranks for all Groups test. The package Statistica 7 was used for all analyses.

(ii) When do tree species germinate?

From September 2002 to April 2003, I walked random transects through the Satara, Lower Sabie and Pretoriuskop region and noted the presence of newly emerged tree seedlings (identified by the presence of cotyledons). During the following wet season I walked ten 50 m long marked transects in the Satara region and ten in the Pretoriuskop region twice monthly from September 2003 to January 2003. The presence of seedlings (identified by the presence of cotyledons) was noted on two metres of either side of the transect line.

During the second wet season (2003) I planted out approximately 600 seeds per species per month (Sep-Dec) of *Terminalia sericea, Peltophorum africanum* and *Combretum hereroense* at the Pretoriuskop site and 600 seeds per species of *Philenoptera violacea, Colophospermum mopane* and *Acacia nigrescens* at the Lower Sabie site. Planting was done in mid-September and again in the middle of October, November and December. One treatment with half of these seeds received approximately 60 mm of simulated rainfall via irrigation immediately after planting in the respective months whilst a second treatment with the remaining 300 seeds of each species received no water. Germination of seedlings was recorded.

(iii) What are the physiological adaptations to drought stress?

Transpiration and leaf (leaflet for *Acacia nigrescens*) temperature were recorded for seedlings of *Philenoptera violacea* and *Acacia nigrescens* in the short rainy season treatment from the time the roofs were erected, on the 19th and 22nd of February and then from the 1st of March for every three days until the 9th of April. Over this time period, the average volumetric soil moisture dropped from 40% to 19%. Leaf temperature (^{0}C) and transpiration (μg cm^{-2} s^{-1}) were recorded using a steady-state Li-Cor porometer (Model LI-1600). Measurements were taken on three large and three small seedlings of both species at 9am and 3pm every third day (Table 2). I allowed five minutes between measurements to allow the Li-Cor porometer to equilibrate to differences in temperature and humidity. Readings were taken 30 seconds after the seedling was clipped to the cuvette to allow the equipment to stabilize. I chose different seedlings at random to reduce damage from handling when clipping the very small leaves or leaflets onto the cuvette.

Statistical Analysis

I used a two-tailed t-test for independent samples to compute differences in leaf temperature and transpiration between size classes and species. In cases where the assumption of homogeneity of variances was violated, a nonparametric Mann-Whitney test was applied.

Table 2 The median number of leaves (*Philenoptera violacea)* and leaflets (*Acacia nigrescens*) for the two size classes, small and big. Standard deviation is indicated in brackets.

Species	*Small*	*N*	*Large*	*N*	*Range*
Philenoptera violacea	4.5 (1.4)	13	8 (2.6)	10	3 - 13
Acacia nigrescens	10 (1.37)	9	25 (37.75)	6	9 - 118

(iv) Do savanna tree species create a seed bank?

I collected ten soil samples from each of the ten transects walked in the Pretoriuskop and Satara region during the middle of September 2003. The soil samples (10 cm diameter, 10 cm deep) were collected from underneath adult trees and in the open after first removing surface litter. I sieved the respective soil samples through a 3 mm sieve whilst spraying with water and removed any seeds present.

Results

(i) Does the length of growth during the rainy season influence dry season survival?

The length of the rainy season did not influence the length of dry season survival. Despite significant differences in seedling size (Table 3) there was no difference in the mean age (number of days since germination) at which death occurred between the long-moist rainy season, long-dry rainy season or the short rainy season treatment for *Acacia nigrescens* (mean = 30 days (st. dev = 69) median = 12 days; $H_{(2, 36)} = 36$, p =0.422) or *Philenoptera violacea* (mean = 41 days (st. dev = 80) median = 15 days; $F_{(2\ 62)} = 1.21$, p = 0.310). There was no significant difference between the two species in the mean age of seedling mortality (mean = 102 days (st. dev = 76); median = 12 days $F_{(5, 96)} = 0.74$, p = 0.59). One seedling of *Acacia nigrescens* died 400 days after

germination and three seedlings of *Philenoptera violacea* died approximately 280, 350 and 400 days after germination (Fig. 2). The late mortality of these few seedlings caused the mean age of seedling survival to be considerably higher (102) than the median age of seedling survival (12).

Acacia nigrescens seedlings of the short rainy season treatment were significantly smaller than the long moist and long dry rainy season treatments ($H_{(2, 219)} = 42.64$, $p = 0.000$) (Table 3). For *Philenoptera violacea* seedling size was significantly different between all treatments ($H_{(2, 2357)} = 501.81$, $p = 0.000$) (Table 3).

Mid rainy season breaks in rainfall and not the dry season caused 90 % of the seedling mortality of *Acacia nigrescens* and *Philenoptera violacea* (Table 3; Fig. 2). Conversely only two seedlings of *Acacia nigrescens* and five seedlings of *Philenoptera violacea* died during the dry season (Fig. 2).

Although the remainder of the species that germinated at the two field sites were not included in the experimental manipulation of the length of the rainy season, mortality recorded for these seedlings also indicate that, apart for *Sclerocarya birrea,* 90 % of all mortality for all these species was incurred immediately after germination (Fig. 2). The older seedlings (more than sixty days since germination) of *Sclerocarya birrea* that died were all seedlings that had germinated late in the wet season (from the end of February to the end of May).

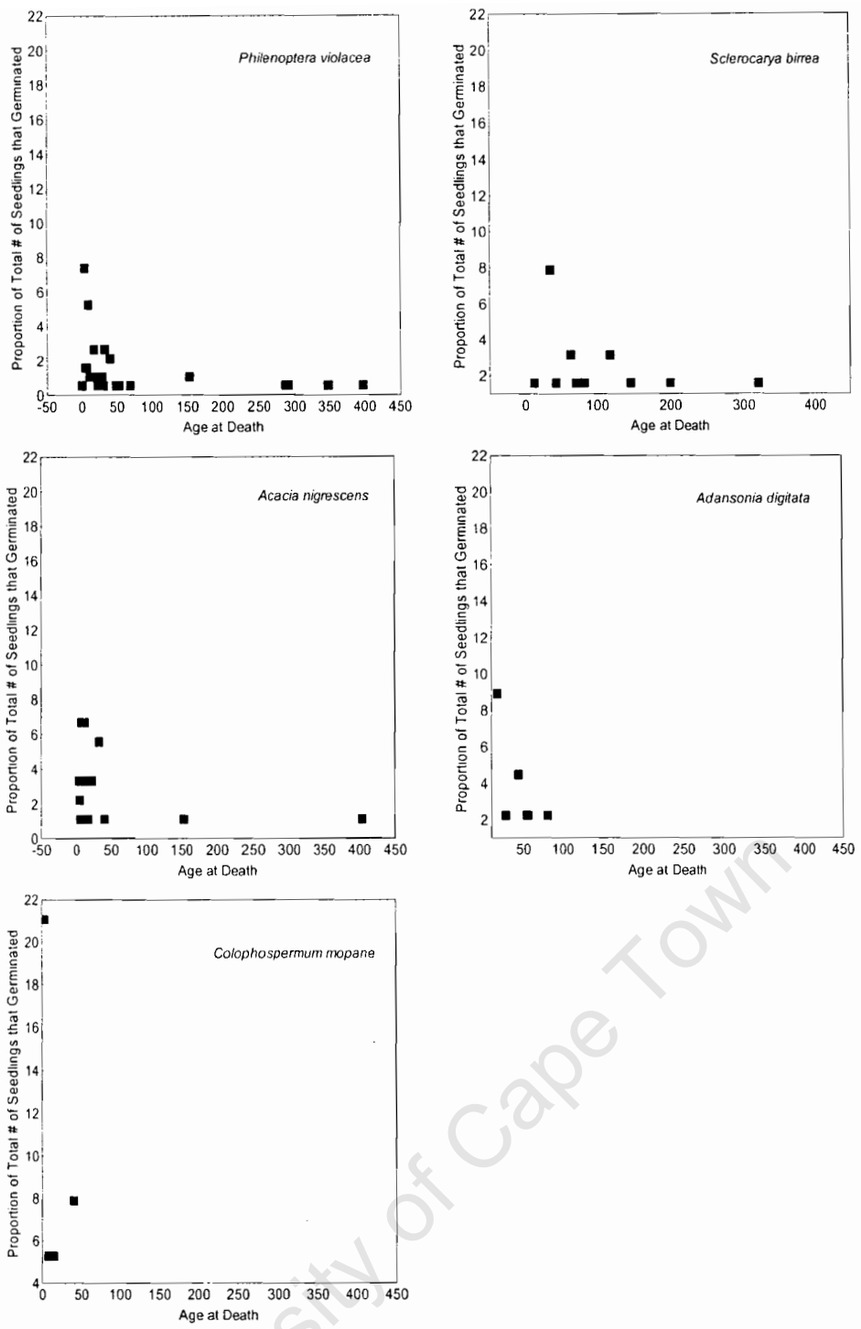

Figure 2 The proportion of seedlings that died at each seedling age for all species across all treatments. Age at death refers to the number of days since germination.

Apart from the long-moist rainy season treatment of *Philenoptera violacea* the volumetric soil water content of the deepest layer of the remaining treatments became equal over the course of the dry season, despite having different soil moisture contents at the end of the rainy season (Fig.3).

Table 3 The mean number of leaves (and leaflets for *Acacia nigrescens*) per treatment and the mean no. of days at which mortality occurred for *Acacia nigrescens* and *Philenoptera violacea.* Significantly different treatments are indicated by the superscript letters ($p < 0.000$).

Treatment	*Mean no. of leaves/ leaflets*	*St. dev*	*df*	*Mean no. of days at death*	*St dev*	*df*
			Acacia nigrescens			
Long-moist rainy season	387^{A}	726	106	39^{C}	100	18
Long-dry rainy season	453^{A}	387	101	12^{C}	5.9	6
Short rainy season	23^{B}	63	40	25^{C}	41.2	12
			Philenoptera violacea			
Long-moist rainy season	7^{D}	5.75	2529	24^{C}	72.71	29
Long-dry rainy season	3^{E}	2.20	213	49^{C}	78.07	26
Short rainy season	3^{F}	2.53	996	56^{C}	100.32	11

(ii) When do tree species germinate?

I found no natural seedling emergence in the field from September 2002 to April 2003 in the Satara or Pretoriuskop region. During the second wet season (September 2003 to April 2004) a mass germination event was recorded in the field transects at Pretoriuskop (also recorded by Euston-Brown, *pers comm.*) for *Terminalia sericea* at the beginning of January, after a period of heavy rainfall. During the same time, newly emerged seedlings of *Sclerocarya birrea* were also recorded in the field transects at Pretoriuskop and at Satara.

Mean peak germination of the species planted at the Lower Sabie site was seven weeks after planting on the 26th of December 2000 (Fig. 4).

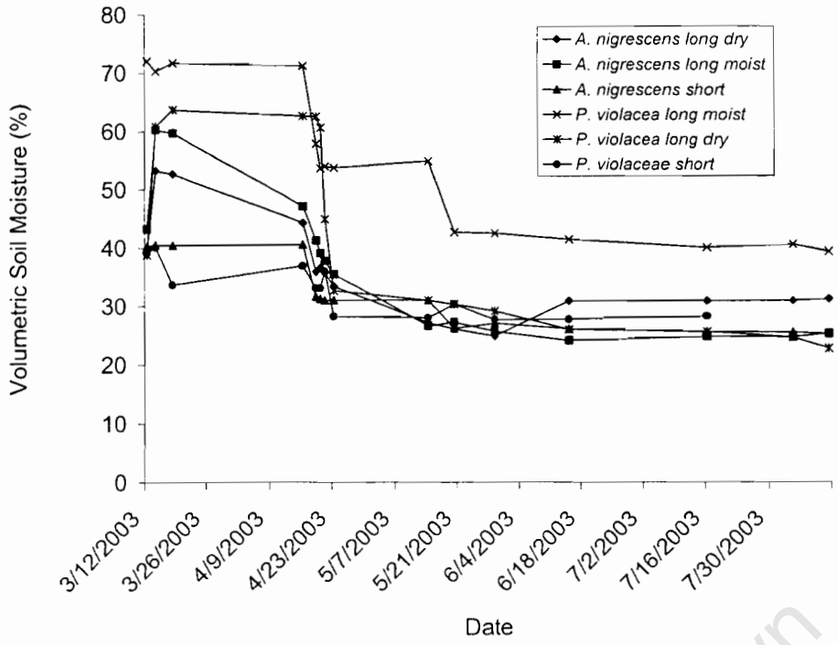

Figure 3 The average volumetric soil moisture (%) across all depths per treatment from the end of the rainy season throughout the dry season.

At the Pretoriuskop site, three large germination events were recorded for *S. birrea* with maximum number of new seedlings counted on the 28th of February 2003 and for *Adansonia digitata* on the 10th of December 2002 (Fig. 4).

For the germination experiment conducted during the 2003 wet season, only *Peltophorum africanum* and *Philenoptera violacea* germinated. Germination for these species was correlated to soil moisture and occurred in the watered plots (60 mm simulated irrigation event) for every month from September to December. No seedlings of *Acacia nigrescens, Colophospermum mopane, Terminalia sericea* and *Philenoptera violacea* were recorded in the watered (60 mm simulated irrigation event) or unwatered treatments. Germination of *Acacia nigrescens* and *Colophospermum mopane* seeds planted in the drought experiment after a large rainfall event and a large natural germination event recorded for *Terminalia sericea* in

the field suggests that a once off 60 mm rainfall event is not sufficient to stimulate germination of these species.

(iii) What are the physiological adaptations to drought stress?

Growth, leaf shedding and transpiration rates

The size attained by seedlings of *Philenoptera violacea* and *Acacia nigrescens* was related to the length of the wet season and soil moisture (Table 3, Fig. 6). Seedlings of *Philenoptera violacea* (Fig. 6a) and *Acacia nigrescens* from the short rainy season treatments had a shorter rainfall season but started to drop their leaves at the same time as seedlings from the long-moist and long-dry treatments. However the length of the growing season (the length of time leaves were retained) varied for different species. All species started to drop their leaves after the last rain in April irrespective of watering regime. However whereas some species had no leaves a month after the rain (*Acacia nigrescens*), some retained their leaves for much longer into the dry season (*Philenoptera violacea*, *Sclerocarya birrea*) and *Colophospermum mopane* seedlings did not drop its leaves at all (Fig. 5-6).

All seedlings of *Sclerocarya birrea, Adansonia digitata* and *Colophospermum mopane* across all plots started to grow new leaves at the start of October 2003 (Fig. 5). For *Acacia nigrescens* and *Philenoptera violacea,* only the seedlings from the long-moist rainy season treatment started resprouting new leaves. The long-dry and short rainy season treatments only started growing new leaves in mid-January 2004. Irrespective of differences in leaf morphology, seedlings of *Acacia nigrescens* and *Philenoptera violacea* had very similar leaf temperatures and transpiration rates (Table 6). *Acacia nigrescens* seedlings shut down transpiration as soil moisture deficit increased (Fig. 7) whereas there was no significant pattern discernable for *Philenoptera violacea* (Fig. 8). *Acacia nigrescens* was also observed to fold leaflets together, which probably acts to shade the leaves as ambient temperature increased. This together with the smaller leaf size of leaflets allowed *Acacia nigrescens*

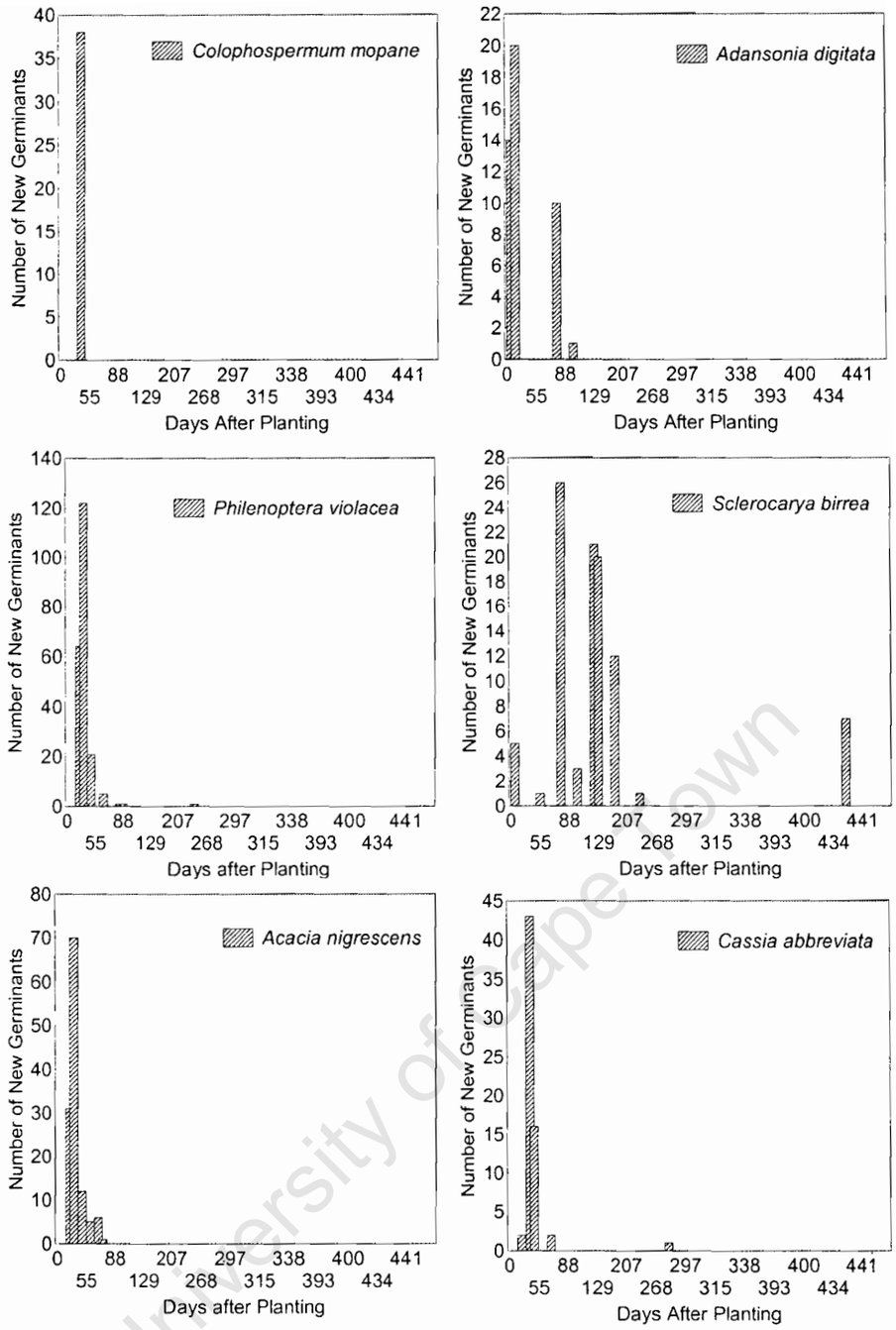

Figure 4 The mean number of seedlings for all species that germinated over time at Lower Sabie and Pretoriuskop. Seeds were planted on the 1st of November at Pretoriuskop and on the 3rd of November at Lower Sabie and represents time zero. The largest germination event recorded for all species occurred after a large rainfall event in December.

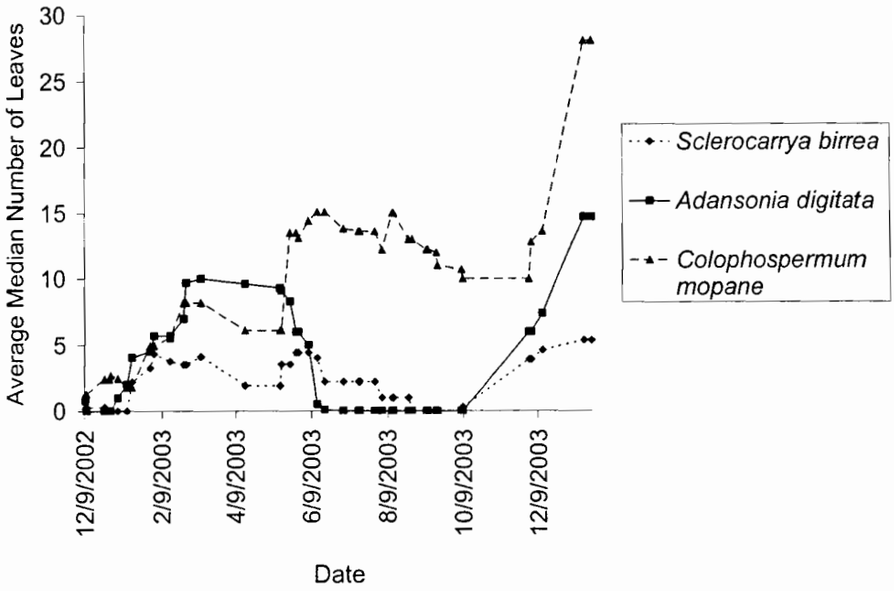

Figure 5 The average median number of leaves for seedlings of *Sclerocarya birrea* and *Adansonia digitata* grown at Pretoriuskop and *Colophospermum mopane* seedlings grown at Lower Sabie over a one year period.

seedlings to minimize leaf temperature increase in the afternoon (~ 2 °C) whereas *Philenoptera violacea* seedlings showed a higher increase (~ 6 °C) (Table 4).

The leaf temperature over the period measured, averaged 33.67 °C (st dev = ± 3.55, n = 180) for all *Acacia nigrescens* seedlings and 32.41 °C (st dev = ± 4.04, n = 180) for all *Philenoptera violacea* seedlings. The transpiration rate over the period measured, averaged 4.93 μg cm^{-2} s^{-1} (st dev = ± 6.82, n = 180) for all *Acacia nigrescens* seedlings and 4.91 μg cm^{-2} s^{-1} (st dev = ± 8.09, n = 180) for all *Philenoptera violacea* seedlings.

Large vs. Small seedlings

There was no significant difference in the average leaf temperature between the large and small seedlings for either *Acacia nigrescens* or *Philenoptera violacea* (Table 4). Similarly, there was no difference in average transpiration rates between the large and small seedlings of *Acacia nigrescens* or *Philenoptera violacea* (Table 4).

When I compared the average transpiration rates and leaf temperatures separately for the morning and the afternoon, there were also no differences between the large and small seedlings of both species (Table 4).

Morning vs. Afternoon

When the morning leaf temperatures were compared with those of the afternoon, both large and small seedlings for both species had significantly higher leaf temperatures in the afternoon (Table 4). When the afternoon transpiration rates were compared with those of the morning, both large and small *Acacia nigrescens* seedlings had slightly lower transpiration rates (difference between afternoon and morning values of -1.09 $\mu g\ cm^{-2}\ s^{-1}$ and -1.22 $\mu g\ cm^{-2}\ s^{-1}$ for large and small seedlings respectively) in the afternoon (Table 4). The transpiration rates for large seedlings of *Philenoptera violacea* were slightly greater in the afternoon than in the morning (difference of 0.69). These differences were not significant (Table 4).

For *Acacia nigrescens* seedlings, there was a significant increase in the number of zero (less than 0.5 $\mu g\ cm^{-2}\ s^{-1}$) transpiration readings from the time the rain-out shelters were erected (Fig. 7). This relationship held when the large seedlings were compared with the small seedlings (Fig. 10b), or the morning readings were compared to the afternoon readings (Fig. 7).

Overall, there was no significant relationship between the number of zero transpiration readings over time for *Philenoptera violacea* seedlings (Fig. 8). Large *Philenoptera violacea* seedlings showed a tendency to have decreased zero transpiration readings after the rain-out shelters were erected, whereas the small-seedlings showed a slight increase in the number of zero transpiration readings over time (Fig. 8).

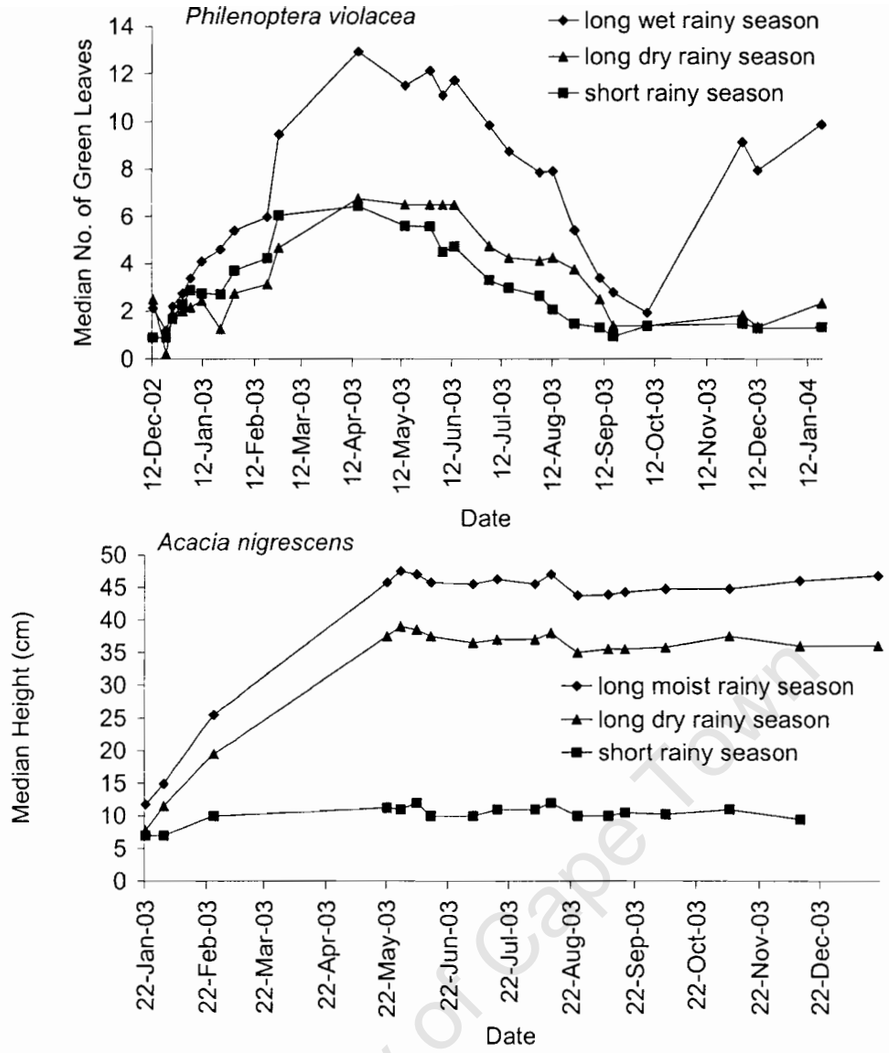

Figure 6 The mean number of green leaves of *Philenoptera violacea* and mean height of *Acacia nigrescens* seedlings across all three treatments.

Table 4 The mean temperature (°C) and mean transpiration rate (μg cm^{-2} s^{-1}) of large and small seedlings of *Acacia nigrescens* and *Philenoptera violacea* in the morning and afternoon. Standard deviation is given in brackets. The test results for significant differences between afternoon and morning readings for large and small seedlings are indicated.

	Afternoon		Morning					
	Large	Small	Large	Small	Afternoon: Large vs Small	Morning: Large vs Small	Large: Aft vs Morn	Small: Aft vs Morn
Temperature (°C)								
A. nigrescens	34.3 (5)	35 (3.3)	32.6 (2.5)	32.8 (2.4)	n.s.	n.s.	**	**
P. violacea	35.3 (3.6)	35.2 (3.2)	29.7 (2.4)	29.5 (2.2)	n.s.	n.s.	**	**
Transpiration (μg cm^{-2}s^{-1})								
A. nigrescens	4. 4 (4.6)	4. 3 (3.3)	5.5 (7.5)	5.6 (10)	n.s.	n.s.		
P. violacea	4.8 (4.6)	6.9 (14.6)	3.5 (2.9)	4.4 (4.1)	n.s.	n.s.	*	n.s.

A similar, weaker relationship was also noted when the morning readings were compared with that of the afternoon. There was a tendency towards more zero transpiration readings over time in the morning whereas a slight decrease in afternoon zero transpiration readings were observed.

(iv) Do savanna tree species create a seed bank?

No seeds were found in any of the soil samples for either Satara or Pretoriuskop.

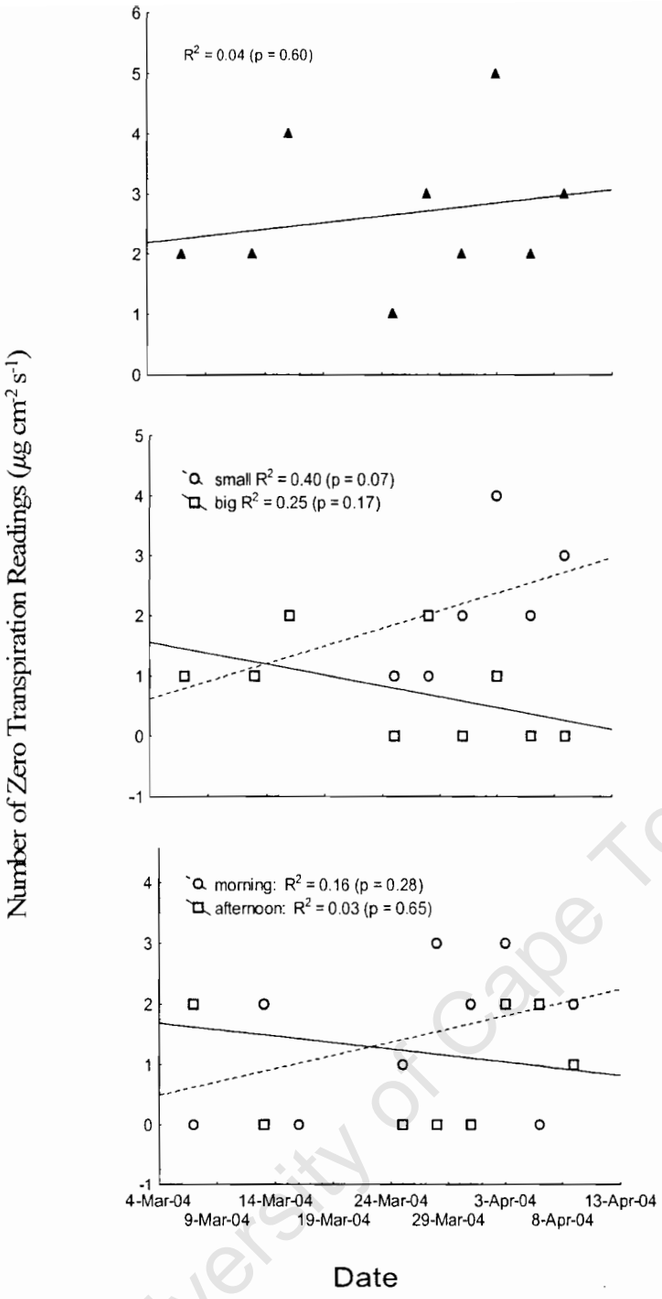

Figure 7 The overall number of zero transpiration readings recorded for *Acacia nigrescens* seedlings from the time the roofs were erected (top graph), compared between small and large seedlings (middle graph) and between the morning and the afternoon readings (bottom graph).

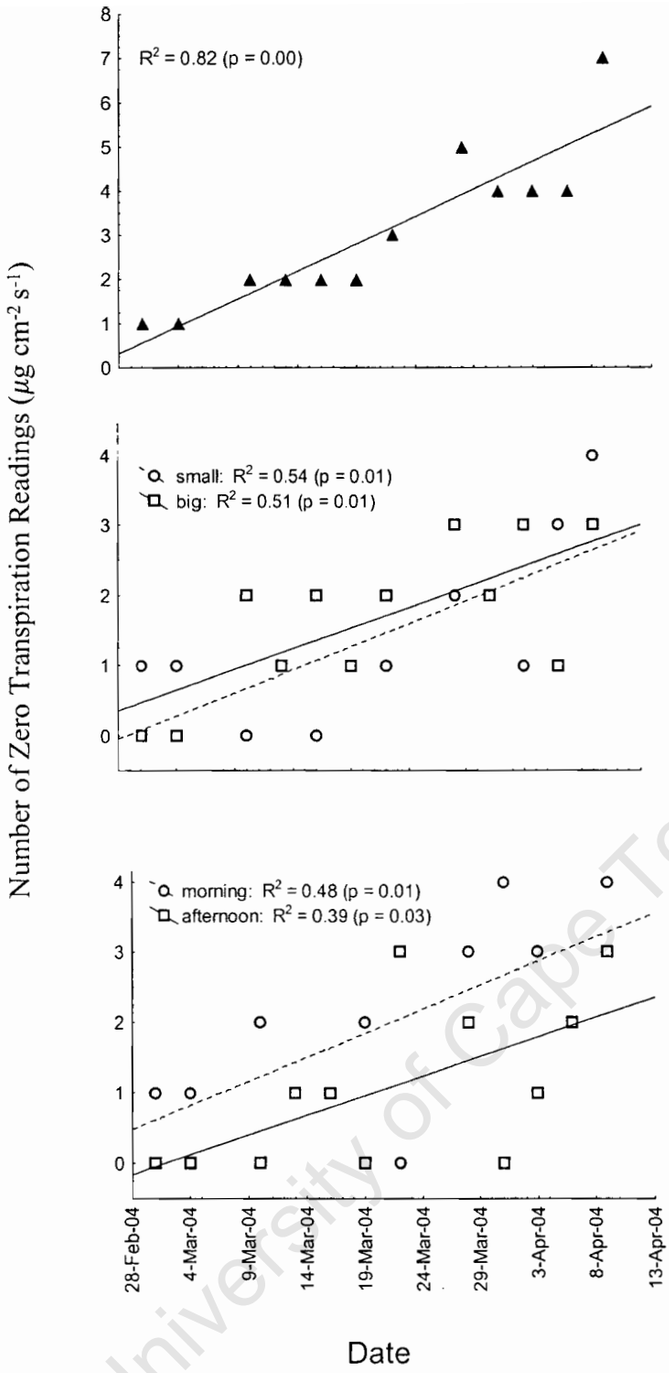

Figure 8 The overall number of zero transpiration readings recorded for *Philenoptera violacea* seedlings from the time the roofs were erected (top graph), compared between small and large seedlings (middle graph) and between the morning and the afternoon readings (bottom graph).

Discussion

Contrary to the idea that seedling establishment should be limited to above-average rainfall years (Barnes, 2001; Harrington, 1991; Keya, 1997; O'Connor, 1995; Scholes & Archer, 1997), survival of *Philenoptera violacea* and *Acacia nigrescens* seedlings that had received a below average rainfall year were no different to that of seedlings that had received an above-average rainfall year.

Although maximum germination during the drought experiment of all species was during a period where the likelihood of follow-up rain was highest (Chapter 3), ninety percent of all seedling mortality occurred within the first sixty days after germination (apart from *Sclerocarya birrea* (44%)). This was despite the fact that I aimed to apply irrigation at optimal intervals between rain events. Only 10% of all seedling mortality for *Philenoptera violacea* and 6% for *Acacia nigrescens* occurred during the dry season. This suggests that mid-term breaks in rain within the wet season (Barnes, 2001; Adiku *et al.*, 1997) as opposed to the length of the dry season may be more critical to successful seedling establishment. It is interesting to note that seeds of most species germinated in reference to large rainfall events rather than to calendar dates. This suggests that the timing of germination has been selected to minimize drought stress in the rainy season rather than to maximize period available for wet season growth. Therefore, in the following chapter, I investigate the drought resistance of seedlings from different species immediately after germination (Chapter 5).

Excavations made throughout the Satara and Pretoriuskop region at the end of the 2003 dry season, supposedly the time most trees have dropped their seeds (Khurana & Singh, 2000), revealed no presence of a seed bank for any species. Hard-seeded species are probably more likely to be adapted to risk-spreading since mechanical scarification like rolling on the ground, may make only a proportion of the seed crop suitable for germination at any given time. However many of the *Acacia* spp. that are hard-seeded are adapted to animal herbivory (Coe and Coe, 1987) and therefore the seed crop in any given year receives similar scarification since the majority of seeds would pass through an animal gut (Miller, 1995). A smaller proportion of seeds that are not ingested may drop to the ground and form a persistant seed bank that becomes germinable through mechanical scarification.

Excavations were made at a time when most trees had no seeds and before the first rains to give an indication of the size of the current year's seed crop. The absence of seeds suggests that seed production of savanna trees are not yearly as has been suggested (Medina and Silva, 1990). Supposedly, adult savanna trees have access to underground water during the dry season and are therefore able to produce seeds yearly (Medina and Silva, 1990). However, seed production could be linked to rainfall from the previous rainy season. Some species also produce seed only with the first rains of the current rainy season and start to drop them a few months later (e.g. *S. birrea; pers. obs.*). For these species poor rains at the start of the wet season may result in a poor seed crop.

The germination of added seeds in the drought experiment and the observed natural germination after a heavy rainfall period in the Pretoriuskop region suggest that the presence of seed would produce seedlings. High herbivore pressure in the Satara region, especially by giraffes that are able to reach high into the tree canopy, may significantly reduce the number of seeds available. The fact that I found no presence of a seed bank and seedlings for only two species in the field across two growing seasons certainly highlights the suggestion that seedling establishment may be limited by seed availability (Clarke & Davison, 2001).

Unlike leaf morphologies, *Acacia nigrescens* and *Philenoptera violacea* seedlings appeared to have similar root morphologies, consisting of a single taproot with very few lateral branches. Developing a root system that extends below the grass layer supposedly enhances the probability of seedling survival through the dry season and is dependant on the length of the rainy season (Medina and Silva, 1990). However dry season seedling survival was high for seedlings of *Philenoptera violacea* and *Acacia nigrescens* irrespective of whether they had received a two-month or four-month long rainy season. Having roots that extend deeper down reduces soil moisture stress since soil moisture generally increased with depth for the clay soils (Chapter 6). In contrast developing deep taproots in sandy soils may not reduce moisture stress since soils dried out throughout the entire soil column (Chapter 6). I observed root thickening for *Sclerocarya birrea* and *Adansonia digitata* which could be an adaptation for surviving

water deficits on sandy soils. Root thickening has been found for *Eucalyptus* species growing on sandy soils in Australia but not on clay soils (Ladiges, 1974).

My study did not consider the effects of grass on seedling establishment since I wanted to find out what the water requirements are for individual seedlings. Shading by grasses could facilitate or suppress seedling growth but would likely reduce the amount of soil water available.

Predictions

The high percentage dry season survival of seedlings suggests seedling roots had sufficient time to penetrate the deeper soil layers, despite the below-average rainfall treatments receiving 200 mm less rain. This suggests that dry season seedling survival is dependant on the probability of seedling roots reaching the deepest soil layer and that this layer does not dry out below a certain threshold.

The high germination fraction after a large rainfall period could suggest that certain savanna seeds cue their germination to periods of heavy rain (Barnes, 2001), where a deep soil moisture recharge of the soil should also aid new roots reaching the deeper soil layers.

Conclusion

Unlike desert succulents, the dry season survival of savanna tree seedlings are not related to the length of the growing season they have received (Jordan & Nobel, 1979). Instead savanna tree seedling survival is dependant on seedling roots reaching the deeper, moister soil layers after germination. The probability of follow-up rain after germination is low (Chapter 3) which suggests that within-wet season dry spells immediately after germination, instead of the length of the wet season, drives episodic recruitment opportunities for savanna tree seedlings.

Chapter 5

Investigating savanna tree seedling vulnerability to rainfall variability immediately after germination

Abstract

Certain savanna tree seedlings are more susceptible to mortality during rainfall-breaks immediately after germination than during the subsequent dry season (Chapter 4). The number of rainfall events that a newly germinated seedling receives may enhance seedling survival if increased number of growth days means that roots are able to reach deeper, moister soil layers. Thus preferential allocation to root biomass compared to leaves and shoot biomass in arid and semi-arid savannas could mean that seedling establishment opportunities are equal for mesic and arid savannas. I grew two species, *Terminalia sericea* and *Sclerocarya birrea* in granite sand and *Acacia nigrescens* and *Philenoptera violacea* in basalt clay in pots. Seedlings were watered for varying number of days after germination before withholding water completely. I found that for *Terminalia sericea* and *Sclerocarya birrea,* but not for *Philenoptera violacea* and *Acacia nigrescens,* an increase in seedling size increased the number of dry days seedlings were able to survive. However none of the species invested proportionally more carbon below ground than to above ground structures. The average length of dry days seedlings could survive immediately after germination was similar for *Terminalia sericea* (71 days), *Acacia nigrescens* (95 days) and *Philenoptera violacea* (96 days) but significantly longer for *Sclerocarya birrea* (171 days) (df = 3, N = 90, F-ratio = Kruskal-Wallis Test H = 40.81, p = 0.00). It is predicted that storage of water in roots may enhance dry spell survival for species found on granite sand where soil moisture does not increase with depth. In contrast survival on basalt clay is related to roots reaching deeper, moister soil depths.

Introduction

Dry spells within the rainy season (September to April) are common in both a semi-arid and semi-mesic savanna site within the Kruger National Park (Chapter 3). Results from my field experiment found that tree seedling mortality was highest immediately after germination despite irrigation to minimize dry spells in-between rainfall events (Chapter 4). Once these seedlings had survived the first sixty days after germination they were capable of surviving much longer periods without rainfall during the dry season (Chapter 4). These results support the notion that variability in the distribution of rainfall within the wet limits the establishment opportunities of savanna tree seedlings (Barnes, 2001; Midgley & Bond, 2001; O'Connor, 1995).

Tree seedlings therefore require enough rain to stimulate germination but also need timely follow-up rain to prevent mortality of newly emerged seedlings (Barnes, 2001). Yet many studies testing drought vulnerability of seedlings first allow a hardening period of a few weeks or years before commencement of the experiment (Clarke and Davison, 1999). Therefore the question of how long a dry spell newly germinated seedlings can survive before mortality occurs and whether this period differs between species, remains unanswered. Furthermore the number of dry days seedlings can survive may be related to the number of follow-up rainfall events seedlings have received (Jordan & Nobel, 1979). Jordan & Nobel (1979) showed that with more growth days, *Agave deserti* seedlings could grow bigger water-holding leaves which allowed them to survive longer dry periods.

For savanna tree seedlings, investment into roots as opposed to shoots or leaves could increase survival of temporary dry periods. This is because higher root: shoot ratios (r: s) would increase the amount of surface area available for water uptake as well as reduce transpiration through smaller leaf area. Partitioning of carbohydrates to processes associated with water uptake instead of carbon acquisition with increased moisture stress has been noted for the seedlings of some species (Choinski & Tuohy, 1991; Johnson, 1996; Otieno *et al.*, 2001) but not for others (Otieno *et al.*, 2001). Seedlings of *Acacia xanthophloea* maintained similar root: shoot ratios with increased water stress, (Otieno *et al.*, 2001) which may explain why this species is generally

found in wet areas alongside rivers, swamps and pans (Schmidt *et al.*, 2002). Maintaining equal r: s ratios would allow trees to maintain relatively high photosynthetic activity, which may allow a competitive advantage in soils that are predominantly wet but would increase the chances of mortality in soils that are predominantly dry. This suggests that species that are able to shift r: s carbon investment under water stress have a competitive advantage in arid regions (Otieno *et al.*, 2001). Thus, unlike the prediction made by Higgins *et al.* (2000) that seedling establishment should be more frequent in mesic compared to semi-arid savannas, species that occur in arid regions may be more tolerant of drought and therefore able to establish as frequently as species that occur in mesic savannas.

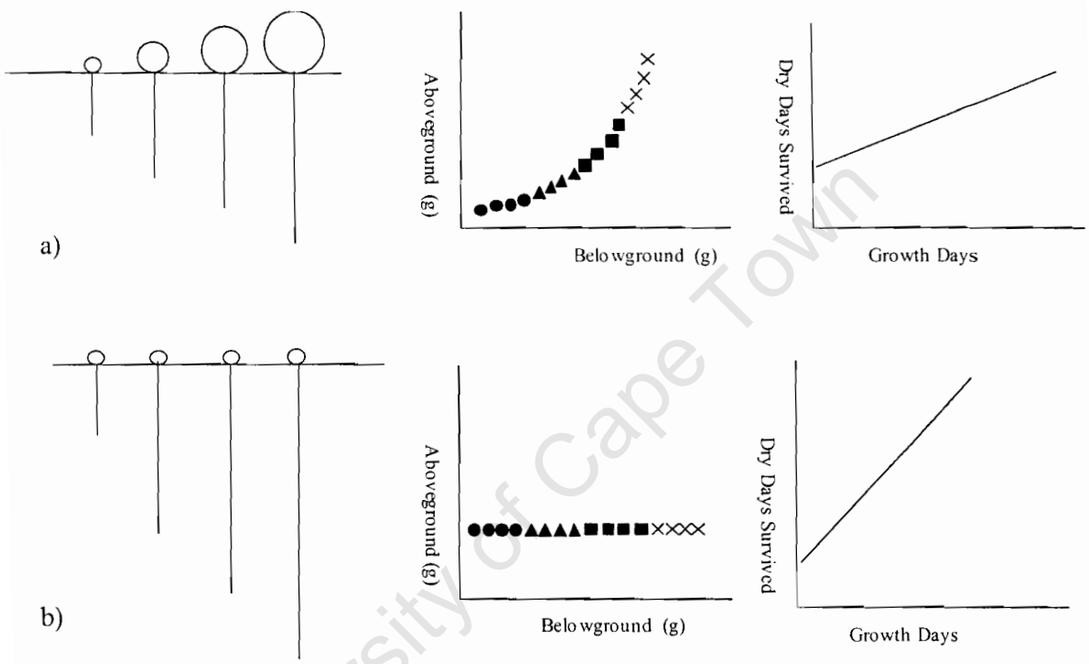

Figure 1 The hypothetical outline of two different seedling strategies, one investing equal proportions of carbon into belowground and aboveground structures (a) versus investing proportionally more belowground (b). Investing more carbon belowground increases the number of dry days a seedling can survive. The number of dry days a seedling can survive increases with the number of growth days it has received.

The aim of this study was to test how long a dry period seedlings can tolerate before they require a rainfall event to prevent mortality. I also tested whether the number of dry days seedlings could survive increased with the number of growth days they have received (Jordan & Nobel, 1979). I did this by growing seedlings in treatments that differed in the number of irrigation events they have received and tested for a relationship with the number of dry days they could then survive. Thirdly I hypothesize that species that invest proportionally more carbohydrates below ground should be able to survive longer without water than species that maintain equal r: s ratios (Fig.1).

Figure one is a graphical representation of this hypothesis. Column one and two displays in picture and in graph format, two different r: s allocation strategies for seedlings hypothetically grown in four different treatments. The treatments differ in the number of growing days seedlings have received. The third column predicts the number of dry days seedlings with a specific r: s strategy would be able to survive to given different amounts of irrigation events. For both strategies the number of dry days they are able to survive increases with the number of growing days they have received. In the first scenario (Fig. 1a) seedlings invest equal amounts of carbon above and below ground. In the second scenario seedlings invest proportionally more resources below ground (Fig. 1b) which allows them to survive a longer number of days without water compared to the first scenario.

Two species that occur in different rainfall zones in the Kruger National Park allow for a unique contrast to test this idea. *Acacia nigrescens* (compound leaves) is dominant in a semi-arid region of the park (Satara) whereas *Terminalia sericea* (broad-leaved) dominates in the semi-mesic part of the park (Pretoriuskop) (Chapter 2). The current distribution of these species may be related to drought tolerance of their seedlings; *Acacia nigrescens* seedlings may have higher r: s ratios compared to *Terminalia sericea*. In addition I included *Sclerocarya birrea* and *Philenoptera violacea,* both of which are widespread within the park (Schmidt *et al.,* 2002).

Methods

Experiment to define tree mortality

I conducted a greenhouse experiment prior to the main drought experiment to determine which drought-induced physical symptoms (colouring, wilting, dropping of leaves) equates to tree mortality. I watered seedlings of each species (*Acacia nigrescens, Philenoptera violacea, Terminalia sericea* and *Sclerocarya birrea*) for approximately a month after which water was withheld. Seedlings in individual pots were re-watered at different stages of wilting. For example, once a seedling displayed leaf wilting, it was re-watered and monitored for new leaf growth. I found that seedlings of all species were able to resprout after their leaves had wilted, turned brown or had been dropped. After the main stem had turned brown, seedlings were able to resprout new leaves if the tip of the stem was still green. Only once the entire stem, including the tip was brown or, in the case of *Sclerocarya birrea,* had become brittle, were the seedlings of all species unable to resprout new leaves.

Drought experiment

Rationale

Seedlings were grown for varying number of days at field capacity (= growth days) after which water was withheld until mortality occurred. The length of the dry period before seedlings died was recorded as "survival days".

Estimation of field capacity

Field capacity is defined as the soil moisture attained after excess water has drained and after the rate of downward movement of water has materially decreased (Wild, 1988). I estimated field capacity in the following manner: I watered all the pots till water ran out the drain holes, after which I sealed the top of the pots with plastic to prevent evaporation. I allowed the pots to drain for one week and weighed them. This weight was taken to be field capacity.

Experimental design

The seedling water stress experiment was undertaken at the University of Cape Town in a glasshouse. Temperatures were milder and humidity lower in the glasshouse than in the Kruger National Park.

Four treatments were set up per species, with 15 pots per treatment. Each 'pot' consisted of a black, vinyl pipe 10 cm in diameter and 40 cm in length. A 10 by 10 cm square plastic bottom with a mesh-covered hole in the middle was glued to one end. To replicate soil conditions in the field, I used basalt clay and granite sand collected from sites in the Kruger National Park. I filled the pots so that the soil at the bottom of the pipes corresponded to the deepest soil layer excavated in the field.

Table 1 The number of seedlings per treatment per species. Percentage germination is given in brackets for each species. The treatment number indicates the number of days seedlings were kept watered before water was withheld completely.

Days at field capacity	***Acacia nigrescens*** *(13%)*	***Philenoptera violacea*** *(19%)*	***Sclerocarya birrea*** *(29%)*	***Terminalia sericea*** *(6%)*
0	7	9	13	5
9				4
18	5	6	11	6
27	5	9	9	5
36	6	9	10	

I soaked the seeds of *Sclerocarya birrea* for two nights and the remaining species for one night in water to which I added seed smoke primer. For *Terminalia sericea* the sharp tip of each seed was cut off with a pair of secateurs. The plugs of *Sclerocarya birrea* seeds were loosened with a pair of sharp scissors. I planted between three to four seeds per species approximately 1.5 cm deep in each pot. I planted *Terminalia*

sericea and *Sclerocarya birrea* seeds in the granite sand and *Acacia nigrescens* and *Philenoptera violacea* in the basalt clay.

Germination was low and each treatment had fewer than the originally planned 15 seedlings (Table 1). All pots were kept at field capacity for 21 days for *Acacia nigrescens, Sclerocarya birrea* and *Philenoptera violacea* and for 53 days for *Terminalia sericea* before the seedlings emerged. Germination was taken as time zero (t0) and seedlings of the first treatment (treatment 0) were dried out from time zero (t0).

The remaining treatments were watered every nine days to field capacity for respectively, 18, 27 and 36 days before being dried out (Table 2), apart from *Terminalia sericea* seedlings which received respectively 0, 9 and 18 days at field capacity (Table 3). Watering every nine days to field capacity is likely to allow some hardening of seedlings instead of suddenly withholding water after a period of being well-watered. Treatment numbers refer to the number of days seedlings were kept at field capacity before being dried out (Table 2 and 3).

Table 2 Watering schedule for the treatments of *Acacia nigrescens, Sclerocarya birrea* and *Philenoptera violacea.* Asterisks indicate watering dates. Time zero (t0) is the day of maximum germination.

Date	*25-Dec 03*	*12-Jan 04*	*21-Jan 04*	*30-Jan 04*
Days since t0	0	18	27	36
Treatment 0	*			
Treatment 18	*	*		
Treatment 27	*	*	*	
Treatment 36	*	*	*	*

Seedlings that were recorded as dead were re-watered and checked to see whether they would resprout to ascertain that they were truly dead. After monitoring the seedlings for 365 days, I terminated the experiment and seedlings that were still alive

on this date were dried out in an oven at 70 degrees Celsius for five days to obtain estimates of dry weight.

Table 3 The watering schedule for the treatments of *Terminalia sericea.* Asterisks indicate watering dates. Time zero (t0) is the day of maximum germination.

	25-Jan 04	03-Feb 04	13-Feb 04
Days since t0	0	9	18
Treatment 0	*		
Treatment 9	*	*	
Treatment 18	*	*	*

Volumetric soil water content of the pots

I watered nine control pots (no seedlings) with basalt clay soil and nine pots with sandy granite soil until water ran out the drain holes. The pots were sealed with a plastic cover, allowed to drain for a day and re-weighed to determine wet weight. I dried the pots in an oven at 100 degrees Celsius for two weeks and re-weighed to determine dry weight. Gravimetric soil moisture content ((wet weight – dry weight / dry weight)*100) was determined to be 35.4% (n=9) for basalt clay and 16.5% (n=9) for granite sand. Average soil bulk density (g / cm^3) calculated as the volume of soil divided by the weight of soil for each pot was 1. 34 g / cm^3 for basalt clay (n = 41) and 1. 46 g/ cm^3 for granite sand (n = 43) respectively. Volumetric soil moisture content (%) was calculated by multiplying gravimetric soil moisture with soil bulk density.

Statistical methods

A one- way Anova was used to test whether there were significant differences between treatments in the number of days seedlings could survive without water. Dry weight comparisons between species were analysed with a simple one-way ANOVA. Where the assumption of homogeneity of variances was violated, a nonparametric

Kruskal-Wallis test was performed. A Tukey Honest Significant Difference post-hoc test was used and, in the case of non-equal variances, the non-parametric Multiple Comparisons of Mean Ranks for all Groups test. The statistical software Statistica 7 was used for all analyses.

Results

Dry Weight

Seedlings of *Sclerocarya birrea* and *Acacia nigrescens* grew significantly bigger the longer they were kept at field capacity as shown by the positive regression relationships between leaf, root and shoot dry weight of these species and number of growth days (Table 4). For *Terminalia sericea* only leaf dry weight and for *Philenoptera violaceae* only root dry weight showed a positive increase with number of growth days (Table 4).

As indicated by the lack of relationship between belowground: aboveground (leaves + shoot) ratios and the number of growth days for any of the species, there was no tendency for any of the species to invest proportionally more carbon to roots than to shoots when they were kept at field capacity for longer before water was withheld (Table 4).

Sclerocarya birrea seedlings had significantly higher dry root weights than the other species despite receiving the same number of growth days (Table 5). Although *Acacia nigrescens, Philenoptera violacea* and *Terminalia sericea* have very different leaf morphologies, there was no difference in carbon allocation to leaves or roots (Table 5). The two species that were grown in the sandy soils (*Sclerocarya birrea* and *Terminalia sericea)* invested nearly equal proportions of carbon into roots as in above ground parts whereas *Acacia nigrescens* and *Philenoptera violacea* that were grown in clay soil invested more carbon into their above ground than their below ground structures (table 5).

Table 4 The regression of leaf, root, shoot and root (r): shoot (s) (leaves + shoot) ratios to number of days grown at field capacity. *, **, *** and n.s. denotes significance differences of 0.05, 0.005, 0.001 and not significant.

Variable	R^2	significance	F - value	n
		Acacia nigrescens		
r: s	0.06	n.s.	1.45	24
leaf	0.59	***	33.28	24
root	0.59	***	40.76	29
shoot	0.6	***	33.28	24
		Philenoptera violacea		
r: s	0.015	n.s.	0.42	28
leaf	0.12	n.s.	3.81	28
root	0.15	*	4.55	27
shoot	0.06	n.s.	1.77	28
		Sclerocarya birrea		
r: s	0.01	n.s.	0.28	38
leaf	0.24	***	11.98	38
root	0.34	***	48.9	38
shoot	0.57	***	18.65	38
		Terminalia sericea		
r: s	0.19	n.s.	4.19	19
leaf	0.38	**	10.93	19
root	0.08	n.s.	1.64	19
shoot	0.07	n.s.	1.45	19

Survival Days

Sclerocarya birrea was the only species with some seedlings still alive after 370 days without water (Fig. 2) whereas all seedlings of *Acacia nigrescens, Philenoptera violacea* and *Terminalia sericea* died within 150 days of last receiving water. Forty five percent of *Sclerocarya birrea* seedlings that had received 27 growth days were still alive after a continuous dry spell of 370 days and over 60% of *Sclerocarya birrea* seedlings that had received 36 growth days were still alive after 361 dry days (Fig. 2). On average, *Sclerocarya birrea* seedlings survived 200 days without water, which

was more than double the average amount of days the other species survived without water (Fig. 3).

There was a trend for seedlings of *Terminalia sericea* and *Sclerocarya birrea* that received more irrigation events to survive longer no-rain periods (Fig. 4). The survivorship curves indicate that the bigger seedlings of *Terminalia sericea* and *Sclerocarya birrea* could survive longer periods without water than seedlings that received fewer growth days. Although there was not complete mortality for treatment 27 and 36 of *Sclerocarya birrea,* the trend of these two treatments appear to be similar to those of treatments 0 and 18, with a higher seedling mortality at the time the experiment was terminated for treatment 27 than for treatment 36 (Fig. 2 and 3). These significant values would have been even larger if I kept the experiment running for longer, allowing the seedlings of treatment 27 and 36 to die naturally.

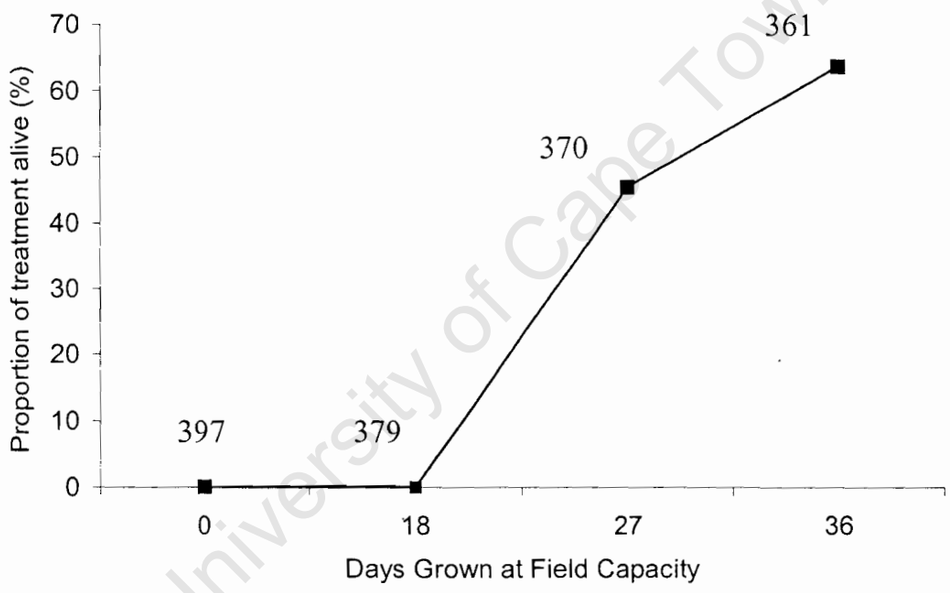

Figure 2 Proportion of *Sclerocarya birrea* seedlings per treatment that were still alive after more than a year without water. The numbers next to the points indicate the number of days the respective treatments had been dried out for.

Table 5 The mean dry weight (g) of the roots, shoots, leaves and the mean below ground: above ground (r: s) ratios for seedlings of *Acacia nigrescens, Sclerocarya birrea, Philenoptera violacea* and *Terminalia sericea* across comparable treatments. Standard error values (SE) are given and significant (sig) differences ($p < 0.05$) are indicated by different letters. Species that share the same letter are not significantly different from each other.

Species	*N*	*Root*	*SE*	*Sig*	*Shoot*	*SE*	*Sig*	*Leaf*	*SE*	*Sig*	*r: s*	*SE*	*Sig*
Acacia nigrescens	14	0.19	0.08	B	0.20	0.03	AB	0.30	0.04	A	0.33	0.03	A
Philenoptera violacea	21	0.28	0.07	B	0.14	0.02	B	0.31	0.03	A	0.66	0.05	AC
Sclerocarya birrea	30	0.77	0.05	A	0.31	0.02	C	0.43	0.03	AB	1.18	0.10	B
Terminalia sericea	16	0.26	0.07	B	0.07	0.02	A	0.25	0.04	AC	1.03	0.11	BC

Treatment 18 of *Terminalia sericea* survived a significantly longer dry spell compared to treatment 0 (Table 6). Those seedlings of *Sclerocarya birrea* in treatment 27 and 36 that were still alive a year after last receiving water were, for the purposes of statistical comparisons, termed to have "died" 370 days after last receiving water. These two treatments survived significantly longer dry days compared to treatment 0 and 18 (Table 6).

Unlike the species grown on sand, there was no clear pattern between growth period and survival period for the seedlings of *Acacia nigrescens* and *Philenoptera violacea* (Fig. 5). The treatment that survived the longest without water for *Acacia nigrescens* was the treatment that received the fewest amount of watering days, treatment 0 (Fig. 5) whereas treatment 36, that had received the most watering survived the second most number of days without water (Fig. 5). For *Philenoptera violacea* treatment 0

and 36 showed 100% mortality on the same day and none of the treatments were significantly different from each other (Table 6).

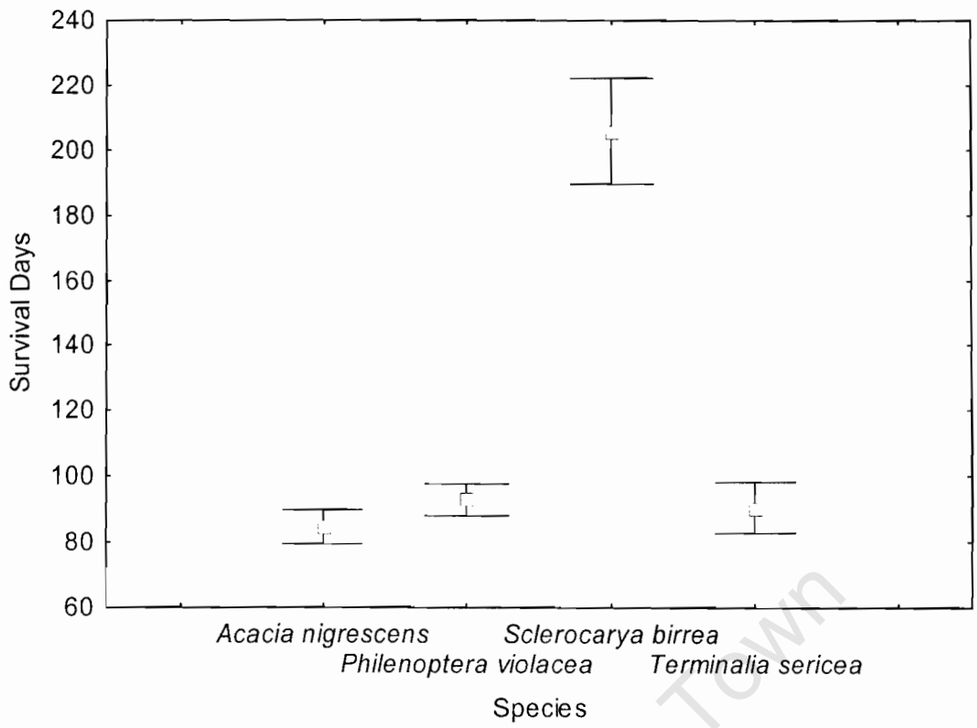

Figure 3 Average number of survival days of seedlings of the different species. *Sclerocarya birrea* seedlings survived significantly more dry days (df = 3, N = 90, F-ratio = Kruskal-Wallis Test H = 40.81, p = 0.00) compared to all other species across comparable treatments.

Volumetric soil water content at death

Across comparable treatments (treatment 0, 18, 27) there was no significant difference (p = 0.13, n = 47) between the volumetric soil water content at which seedlings of *Terminalia sericea* (average = 3.72 %) and *Sclerocarya birrea* (average = 2.1%) died (Fig. 6). Similarly, across comparable treatments (treatments 0, 18, 27, 36), no significant difference (p = 0.197, n = 49) was found between the volumetric

soil water content at which seedlings of *Acacia nigrescens* (average = 15.92%) and seedlings of *Philenoptera violacea* (average = 14.36%) died (Fig. 7).

Table 6 The One-way Anova testing for significant differences (sig) between the number of dry days seedlings of different species could survive when they were grown at different number of days at field capacity after germination. When there were significant differences between treatments, the treatment that survived the longer dry period is mentioned first. *, **, ***, n.s. denotes significant differences of 0.05, 0.01, 0.001.

Species	***Treatments***	***F - ratio***	***df***	***sig***
Acacia nigrescens	t0 from t18	5.316	3	***
Philenoptera violacea		0.250	3	n.s.
Sclerocarya birrea	t36 from t0 and t18	8.68	3	**, **
	t27 from t0 and t18			*, *
Terminalia sericea	t18 from t0	6.29	2	**

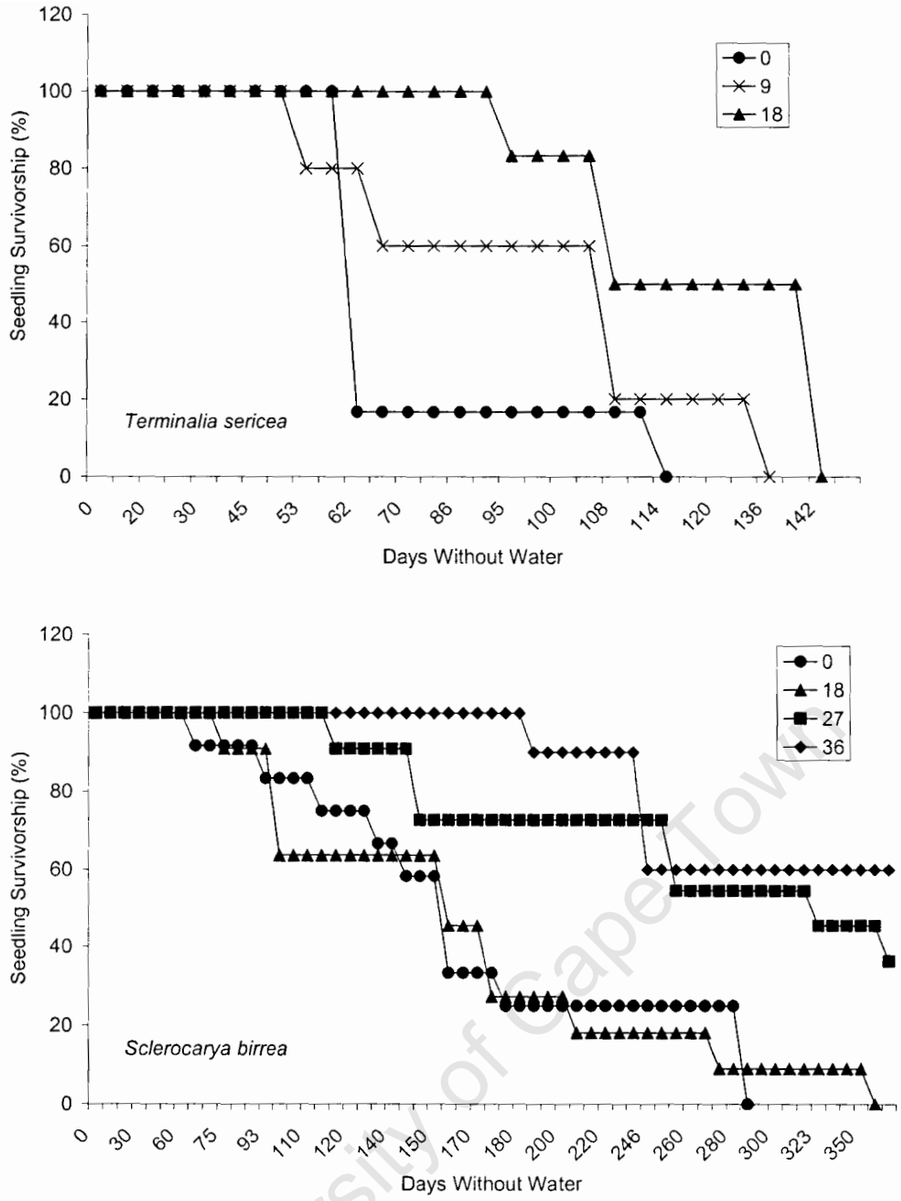

Figure 4 The proportion of seedlings that died after last receiving water for the different treatments grown on granite sand. The number of the treatment indicates the number of days seedlings were kept at field capacity before watering was stopped, e.g. treatment 0 received no further irrigation immediately after mean maximum germination, whereas treatment 18 was kept at field capacity for 18 days after mean maximum germination before further water was withheld.

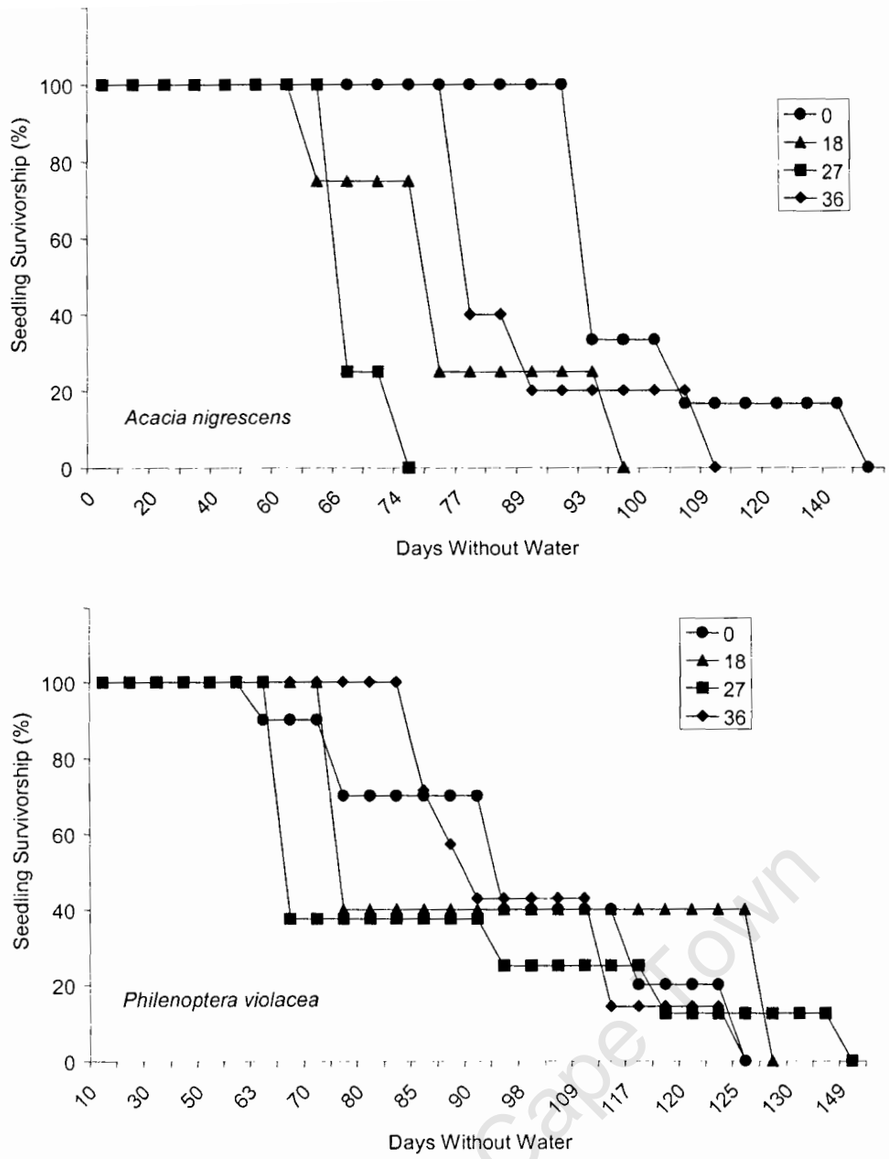

Figure 5 The proportion of seedlings that died after last receiving water for the different treatments grown in basalt clay. The number of the treatment indicates the number of days seedlings were kept at field capacity before watering was stopped, e.g. treatment 0 received no further irrigation immediately after mean maximum germination, whereas treatment 18 was kept at field capacity for 18 days after mean maximum germination before further water was withheld.

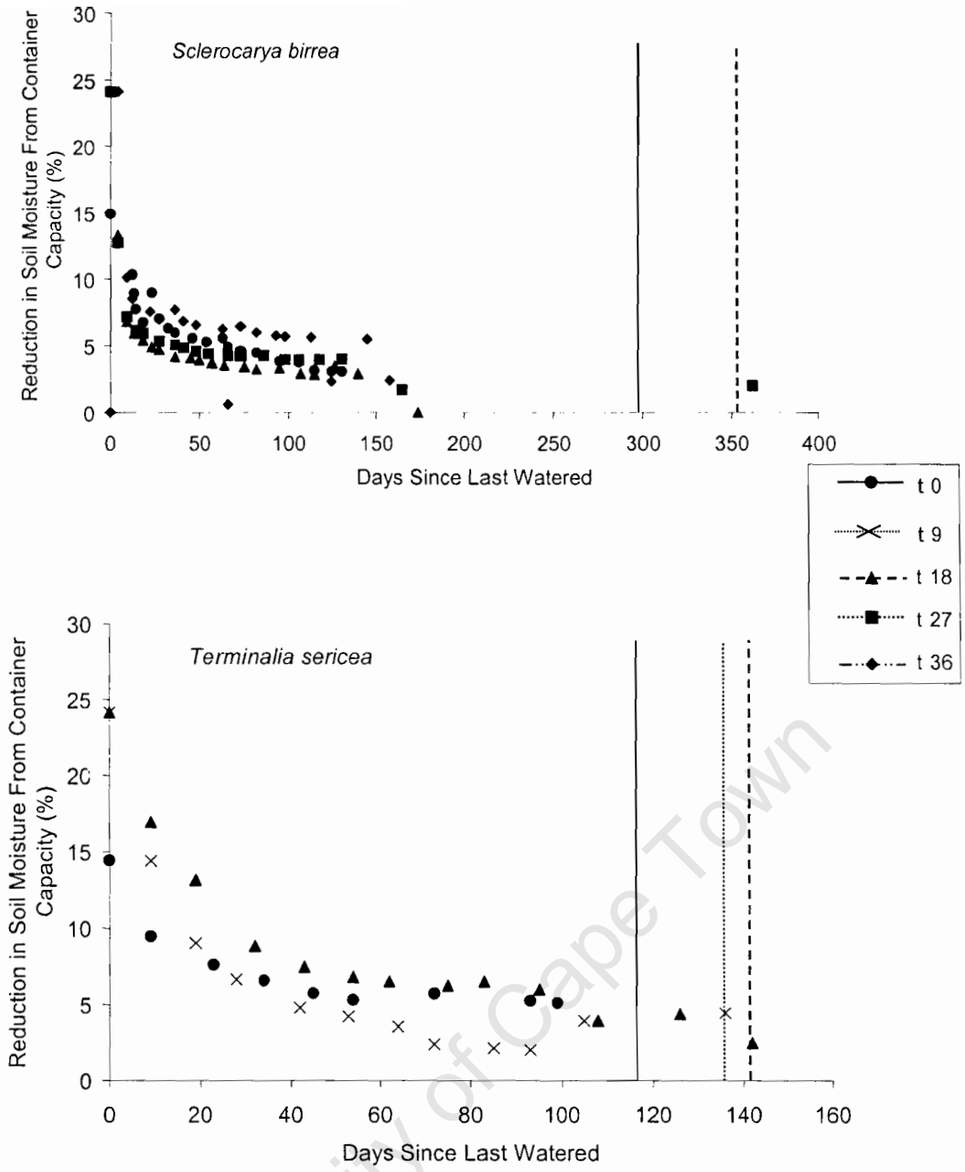

Figure 6 The reduction in volumetric soil moisture from the last time the pots were last watered to field capacity for the various treatments.

Discussion

The number of dry days seedlings could survive after receiving just enough water to germinate was remarkable. The last *Terminalia sericea* seedling that received no more water immediately after germination (emergence of the cotyledons above the soil surface) died 114 dry days later (average of 71 days for treatment 0) (Fig. 4), the last seedling of *Sclerocarya birrea* survived 282 dry days (average of 171 days for treatment 0) (Fig. 4), 145 dry days for *Acacia nigrescens* (average of 95 days for treatment 0) and 125 days for *Philenoptera violacea* (average of 96 days for treatment 0) (Fig. 5). The significantly greater drought survival of *Sclerocarya birrea* compared to the other species (Fig. 3) may be related to its bigger seed size which allows it to grow significantly more root biomass (Table 5) over the same amount of time as the other species.

Although I predicted that species that have high r: s ratios would be able to survive longer no-rain periods than species that maintained equal ratios (Fig. 1), none of the species followed this scenario. Instead all species had similar r: s ratios across the different watering treatments.

Although seedlings of all species showed a remarkable capacity to survive extended no-rain periods, more irrigation events after germination enhanced survival for *Terminalia sericea* and *Sclerocarya birrea* (Fig. 4, Table 6) seedlings but not for *Acacia nigrescens* or *Philenoptera violacea* (Fig. 5, Table 6). This is despite the facts that, like *Terminalia sericea* and *Sclerocarya birrea*, *Acacia nigrescens* and *Philenoptera violacea* seedlings grew bigger root systems with more irrigation (Table 4) and were comparable to *Terminalia sericea* in carbon allocation to their roots (Table 5). *Acacia nigrescens* and *Philenoptera violacea* seedlings had lower r: s ratios compared to seedlings of *Terminalia sericea* and *Sclerocarya birrea* despite receiving similar amounts of irrigation (Table 5). Seedlings of *Sclerocarya birrea* and *Terminalia sericea* could have higher root: shoot ratios to compensate for the lower nutrient status of the granite soil compared that of the basalt clay (Ladiges, 1974).

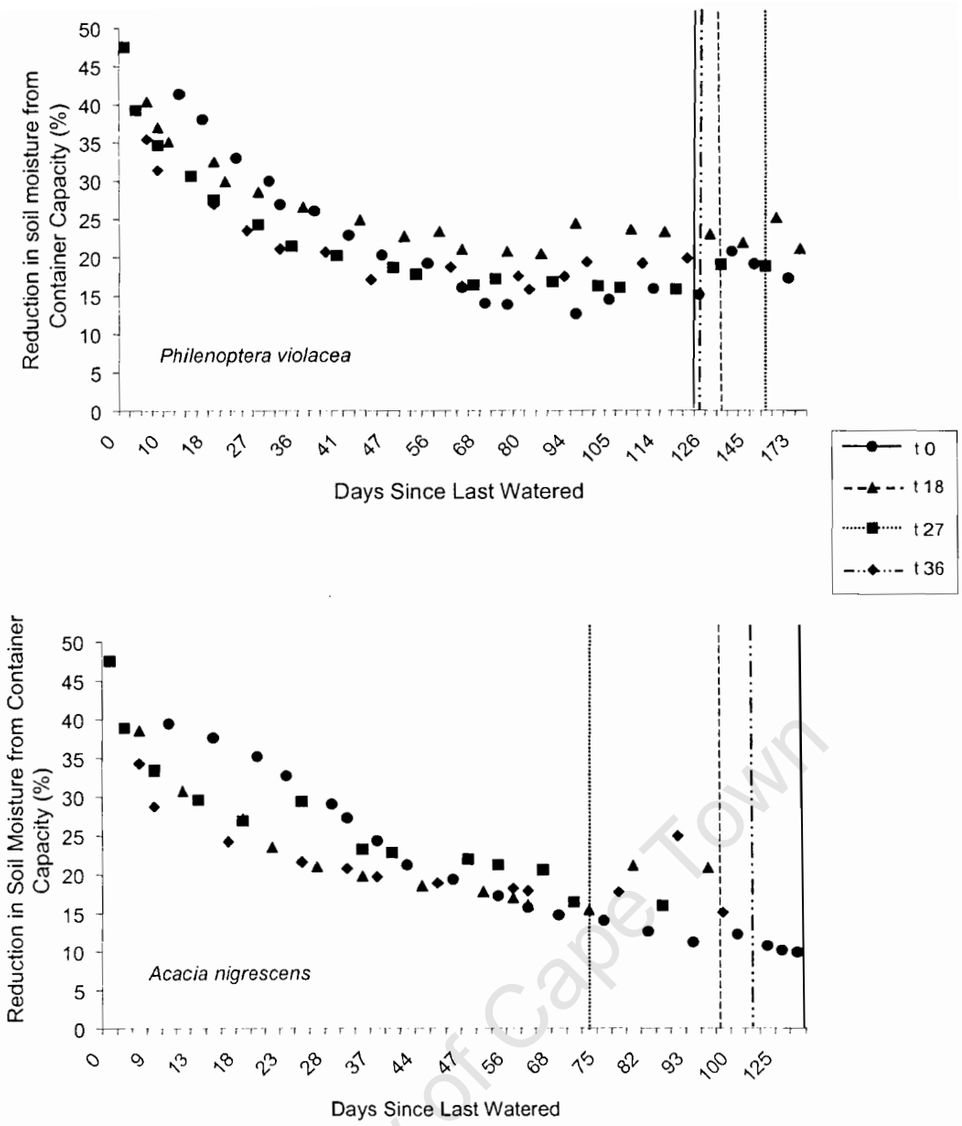

Figure 7 The reduction in volumetric soil moisture from the last time the pots were watered to field capacity for the various treatments.

Similar to the field experiment (Chapter 3), seeds of *Sclerocarya birrea, Acacia nigrescens* and *Philenoptera violacea* germinated at the same time. Seeds of *Terminalia sericea* germinated approximately a month later than the other species. It is possible that the seed of *Terminalia sericea,* which comprises of a woody capsule, requires substantial amounts of water for the capsule halves to swell up and open, thus

"freeing" the emerging radicle. A massive germination event after a period of extended rain was also observed for *Terminalia sericea* in the Pretoriuskop region, Kruger National Park (Chapter 3; Euston-Brown, *pers. comm*). This capsule adaptation would ensure that seeds germinate during extended wet periods in the field, which means the taproot will be extending through wet soil.

Seedlings of *Terminalia sericea* and *Sclerocarya birrea* died at the same volumetric soil moisture contents across treatments despite very different leaf morphologies and seedling sizes (table 5). The same was observed for seedlings of *Philenoptera violacea* and *Acacia nigrescens* grown on the clay soils. These findings can be explained when one looks at the rate at which the pots dry out. For the granite sandy soils, the volumetric soil moisture content started to decline from the last time the pots were watered, dropping from saturation to approximately -5 % of saturated water content in approximately 40 days, irrespective of the species (Fig. 6). At this level no more reduction in pot soil moisture was noted, which suggests no more soil water was available for evaporation or transpiration. The seedlings of *Terminalia sericea* and *Sclerocarya birrea* were able to withstand these dry conditions for varying amounts of time before mortality occurred (Fig. 4). Thus although seedlings of *Sclerocarya birrea* were able to withstand longer periods of no soil moisture availability compared to seedlings of *Terminalia sericea,* seedlings of both species died at the same volumetric soil moisture content.

The same trend was observed for the basalt clay soils (Fig. 7). The soil moisture content dropped from saturation to -15 and –10 % of saturated water content for both species approximately 50 days after last receiving irrigation (Fig. 7). Seedlings of both these species survived at this soil moisture levels for various amounts of days before dying (Fig. 5).

Predictions

In the greenhouse study observed mortality of *Acacia nigrescens* and *Philenoptera violacea* occurred once the soil dropped below a moisture threshold but was not

related to seedling size. This suggests that seedling survival of these species depends on suitable soil moisture conditions during the dry season irrespective of the number of growing days they have received. In contrast, bigger seedlings of *Terminalia sericea* and *Sclerocarya birrea* were able to survive longer dry spells and therefore seedling establishment for these species should be related to the number of growth days therefore total wet season rainfall amount.

Conclusion

Seedling survival is driven by soil moisture and not number of growth days for *Acacia nigrescens* and *Philenoptera violacea* grown on basalt clay soils. In contrast number of growth days increased survival days for *Terminalia sericea* and *Sclerocarya birrea* seedlings. All species required a number of irrigation events to stimulate germination which suggests that seeds are adapted to germinate given that the soil moisture is kept high for a period of time. A single heavy rainfall event or a number of consecutive smaller events (Barnes, 2001) that has the effect of keeping soil moisture high for a sufficient amount of time, should therefore stimulate germination.
This strategy would enhance seedling survival by ensuring that seedling roots are penetrating moist soil layers.

Chapter 6

Determining the frequency of savanna tree seedling establishment

Abstract

It is commonly assumed that seedling establishment in savannas is episodic and related to rare suitable rainfall years. However the frequency of suitable years and occurrence of potential recruitment episodes has not been studied previously. I used a soil-water model to determine how the interaction between rainfall, soil substrate and the presence/absence of grass influences the probability of savanna tree seedling establishment. I combined the results from the soil-water model with past rainfall records to determine the possible frequency of large and small establishment events for a semi-arid savanna site (Satara) in the Kruger National Park. Sixteen of the past 57 rainfall years had soil moisture conditions conducive for possible tree seedling establishment events at Satara. A high probability of large germination and survival of seedlings in March may be related to the occurrence of tropical cyclones of the Indian Ocean that cause large rainfall in the Kruger National Park. Grasses facilitate soil moisture conditions suitable for large germination events but reduce the number of possible establishment events by reducing soil water through transpiration. It is predicted that different seedling strategies are required for survival on granite versus basalt clay soils because of the higher variability in soil moisture on the granite sands.

Introduction

Observations of savanna tree seedling establishment under natural conditions are often reported to be rare (Barnes, 2001; Hoffman, 1996) and therefore establishment events have been suggested to occur episodically and are limited to a few years with above-average rainfall (Harrington, 1991; Jordan & Nobel, 1979; O'Connor, 1995; Walker *et al.*, 1984). Evidence for rainfall-driven periodicity in tree seedling establishment exists (Harrington, 1991; Jordan & Nobel, 1979; Medina & Silva, 1990; Wiegand *et al.*, 1995; Wiegend *et al.*, 1995; Wilson & Witkowski, 1998). For example, Harrington (1991) suggested that only six out of the past 97 years had the correct rainfall distributions that would have allowed for the widespread establishment of *Dodonaea attenuata.* The observed even-sized tree cohorts for some species (Young & Lindsay, 1988) may illustrate the occurrence of rare establishment events whereas staggered cohorts may suggest continuous recruitment (Midgley & Bond, 2001).

Rare episodic tree seedling establishment may also contribute to co-existence of grasses and trees in xeric savannas (Higgins *et al.,* 2000). The model produced by Higgins *et al.,* (2000) suggests that increased probability of dry spells within the growth season in arid savannas limits opportunities for tree seedling establishment. Rare seedling establishment limits tree population because the low tree recruitment rate never allow their densities increasing to a woodland state (Higgins *et al.*, 2000). Despite low recruitment rates, trees are maintained in dry savannas because of the low mortality rate of tree adults allowing for the co-existence of trees and grasses.

The idea that all change in savanna tree densities occur during episodes has been questioned. High germination and survival during a below-average rainfall year ((Brown & Archer, 1999) and a combination of episodic and smaller continuous recruitment (Wiegand *et al.,* 2004; Watson *et al.,* 1997) has been reported. In the case of Watson *et al.,* (1997) large recruitment events occurred during three wet years whilst smaller recruitment events were recorded throughout a seven year drought.

The frequency of seedling establishment will also be influenced by the interaction between the soil substrate and rainfall (Coughener & Ellis, 1993; Medina & Silva,

1990). For example, the high rainfall area of Pretoriuskop has deep granite sand with fast drainage rates and low water retention capacity across all measured depths. In contrast the low rainfall area around Satara is underlain with basalt clays which are shallower, dry out more slowly and have increased soil water retention with depth (Chapter 4). Seedling establishment may be hampered on the granite soils despite the higher mean annual rainfall because seedling root growth is slower than the rate at which the soil dries out (Chapter 4). On the other hand there is a higher intensity of flooding and reduced infiltration during large rainfall events on basalt clays (Medina & Silva, 1990).

Although sufficient soil moisture is critical to successful seedling establishment, a multitude of different factors should interplay with rainfall to allow recruitment (Wiegand *et al.,* 1995). These include a timely fire regime that does not destroy the potential seed crop (Williams, 1999) or newly emerged seedlings (Hoffman, 1996), standing grass biomass that may compete or facilitate (O'Connor, 1995) seedling survival, and herbivory of the seeds (Miller, 1995) and seedlings.

Furthermore, the right rainfall requirements for any given year may occur in a particular way or probably in a combination of different ways to allow for seedling establishment. Seedling establishment may also be uncoupled from rainfall and dependant on specific micro site conditions (Jeltsch *et al.*, 1998) or large reduction in herbivore densities (Prins & van der Jeugd, 1993). Episodic establishment of *Acacia tortilis* was correlated to die-back of impala during anthrax outbreaks in Tanzania (Prins & van der Jeugd, 1993).

However the rainfall analysis (Chapter 3) and the field (Chapter 4) and greenhouse (Chapter 5) experiments I conducted suggest that seedling establishment is more likely under specific soil moisture conditions (Chapter 3; Chapter 4). These results (Chapter 3; Chapter 4) can be used as a guideline to define soil moisture criteria for when establishment at the study areas (Pretoriuskop and Satara) would be most probable. Given that seedling establishment is more probable under certain soil moisture conditions, the aim of this chapter is to determine the frequency of possible establishment events and whether this differs between two sites with different mean annual precipitation and soil types.

During the greenhouse and field experiments I ignored the potential effect of grasses because I was interested in defining the soil moisture conditions required for seedling survival. Interactions between rainfall and grass biomass may have a positive or negative influence on tree seedling establishment. Sufficient water availability during high rainfall years may allow tree establishment because of reduced competition between grasses and tree seedlings (Scholes & Archer, 1997). O'Connor (1995) found grasses facilitate establishment of *Acacia karroo* seedlings in average rainfall treatments whereas seedling mortality of *Prosopis glandulosa* was attributed to grass competition over years of below-average and near-average rainfall (Jurena & Archer, 2003). In this study I test whether grasses facilitate (for example by shading that reduces evaporation) or compete with tree seedlings for available soil moisture by running a soil-water model with and without grass growth.

Here I test whether the co-existence of trees and grasses can be explained by less frequent establishment frequencies in a semi-arid compared to a semi-mesic savanna and whether hydraulic characteristics of the soil substrate affect establishment frequency. To do this I use a soil-water model (WaterMod 3, Greenhat software) to determine how many past rainfall years, had soil moisture conditions conducive for tree seedling establishment, for a semi-arid basalt clay savanna (Satara) and a semi-mesic granite sand savanna (Pretoriuskop) respectively (see Chapter 2 for site descriptions).

The chapter is divided into three parts:

1. Verification of the soil-water model: The predicted soil moisture produced by WaterMod is tested against measured soil moisture data from the field experimental sites on basalt clay and granite sand (Chapter 4).
2. Defining what soil moisture conditions are required for seedling survival. I describe the rationale behind the soil moisture criteria I consider necessary for germination and seedling survival.
3. Combining the soil moisture criteria that are conducive for seedling establishment with the soil-water model to predict which rainfall years, would have been most conducive for tree seedling establishment in the presence and absence of grass growth.

Methods

Verification of the soil-water model

The crop-soil-water programme, WaterMod 3 (Greenhat software) was used. Watermod is a biophysical crop simulation model that focuses on the dynamics between crop water use and soil water. User-specified parameters of climate, soil and crop allow exploration of the behaviour of the biophysical system allowing comparison of simulations with measured data. The input parameters required for WaterMod are discussed in Appendix A.

To parameterize the model the predicted soil moisture was correlated against measured soil moisture data obtained from a capacitance probe that determines volumetric soil moisture at 10 cm intervals (Sentek Diviner 2000 capacitance probe (Chapter 4)). I ran the model repeatedly adjusting soil hydraulic parameters (Appendix A) to improve on the fit between simulated and measured soil moisture. Soil hydraulic conductivity test results for the Pretorisukop granite sand soil and the Satara basalt clay soil were obtained from the Tree-Grass Project (*L. Rademan, project co-ordinator, Tree-Grass Project,* KNP) and used to compare with the soil hydraulic conductivity results generated by WATERMOD. The set of parameters that gave the best regression fits of predicted to actual soil moisture was used to infer soil moisture for past rainfall years.

Results of the verification of the soil-water model

For the basalt clay soil there was a strong, significant relationship between the volumetric soil moisture content predicted by the model and the measured volumetric soil moisture content (%) as determined using the capacitance probe across all depths (Table 1, Fig. 1).The strong 1:1 (intercept 0) relationship (Table 1, Fig. 1) also indicates that the values produced by the model have similar ranges to those of the measured soil moisture values (Fig.1). The 1:1 relationship improves with depth (Table 1, Fig. 1) which could be attributed to the smaller, slower fluctuations in soil water with increased soil depth (Fig. 3, as indicated by the min-max bars).

The results for the model for the granite sands were not as good a fit as on the basalt clay (Table 1, Fig. 2). The problem revolved around setting the soil hydraulic parameters in WaterMod so that it simulated a volumetric soil moisture content that, unlike the basalt clay, had large equivalent increases in soil water content across all depths. The model could also not produce the range of soil moisture which each depth displayed in the field. This is indicated by the large min-max bars in Fig. 3 and by the larger range of measured soil moisture on the x-axis compared to that of the predicted soil moisture on the y-axis across all depths in Fig. 2. Furthermore all soil layers dry out at a very rapid rate across all depths, i.e. the deeper layers do not stay moister for longer or have higher average soil moisture than the shallow layers (Fig. 3).

This may be partly explained by the differences in saturated hydraulic conductivities between the basalt clay and granite sands. Saturated hydraulic conductivity is measured as the flux of water through freely draining soil. Unlike the basalt clays, saturated hydraulic conductivity increased with depth for granite sandy soils at Pretoriuskop which may prevent the retention of increased soil moisture with depth (Fig. 3). Saturated hydraulic conductivity measured for basalt clay decreased from 111 cm/ day at the surface to 20 cm/ day at 30 cm depth compared to 320 cm/ day measured at the surface of the granite sand to 800 cm/ day at 1 m depth. These differences in saturated hydraulic conductivity may be related to high macro-pore density in the granite sand which allows for very fast drainage rates that the model is unable to simulate (*E. Hoffman, Agronomy Dept, University of Stellenbosch, pers. comm.).* Although there is a significant 1:1 relationship between the predicted and measured soil moisture across all depths for the granite sand (Table 1) the observed values have too small a range to allow accurate predictions of suitable soil moisture conditions for seedling survival (Fig.2 as indicated by the difference in range between the x-axis and y-axis). For this reason WaterMod was only used to infer soil moisture for past Satara rainfall records.

The rainfall records were obtained from the permanent weather station at Satara and from Kruger National Park Scientific Services (Nick Zambatis, *pers. comm.*). Years with more than five days of missing data were not considered suitable for analysis.

The final data set comprises the years 1933 to 1952, 1954 to 1959, 1967 to 1976 and 1978 to 2002 for a total of 57 years.

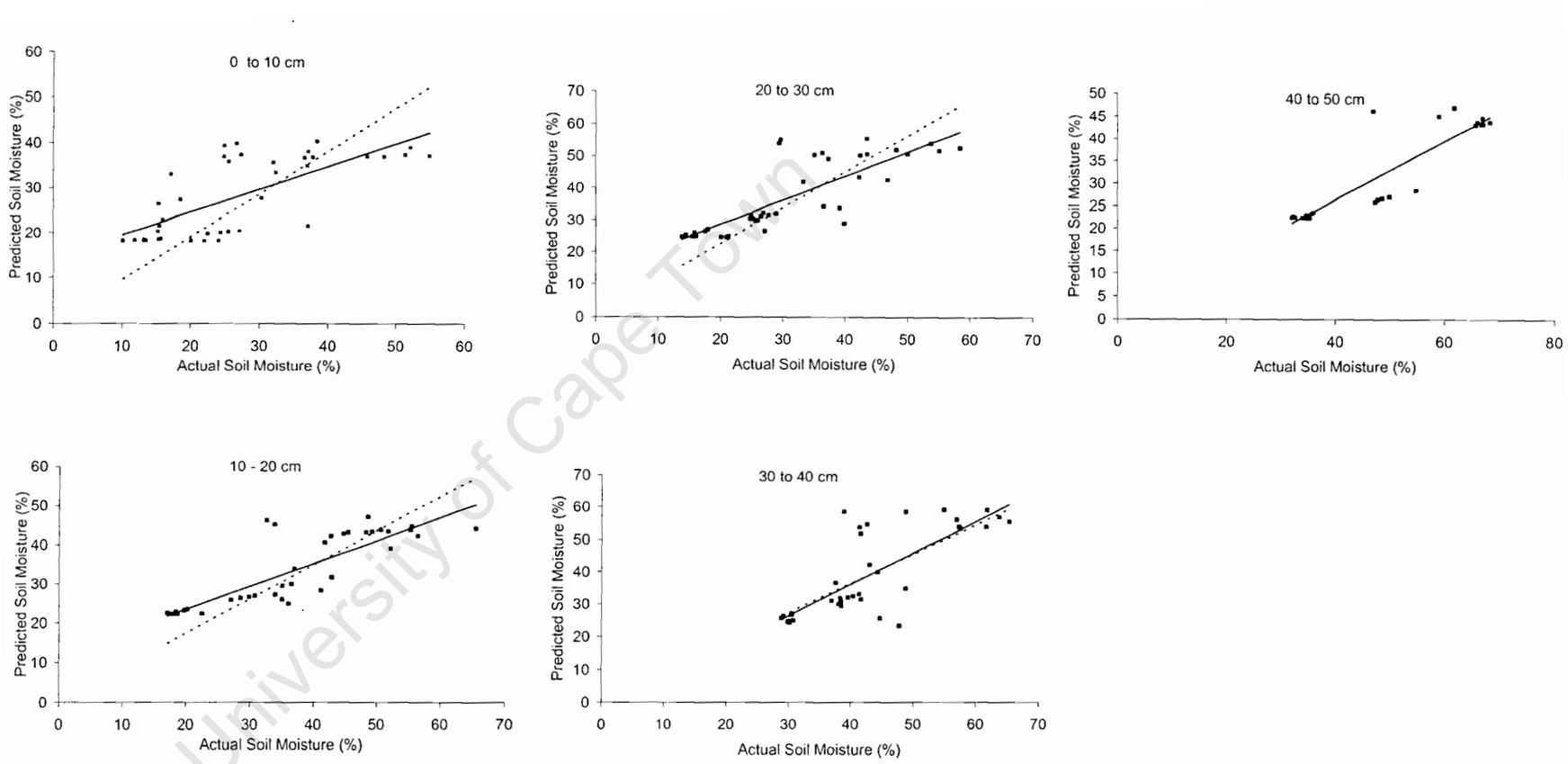

Figure 1 The relationship between predicted and measured soil moisture values for the basalt clay soil for the different depth layers. The dotted line indicates the regression line through the intercept.

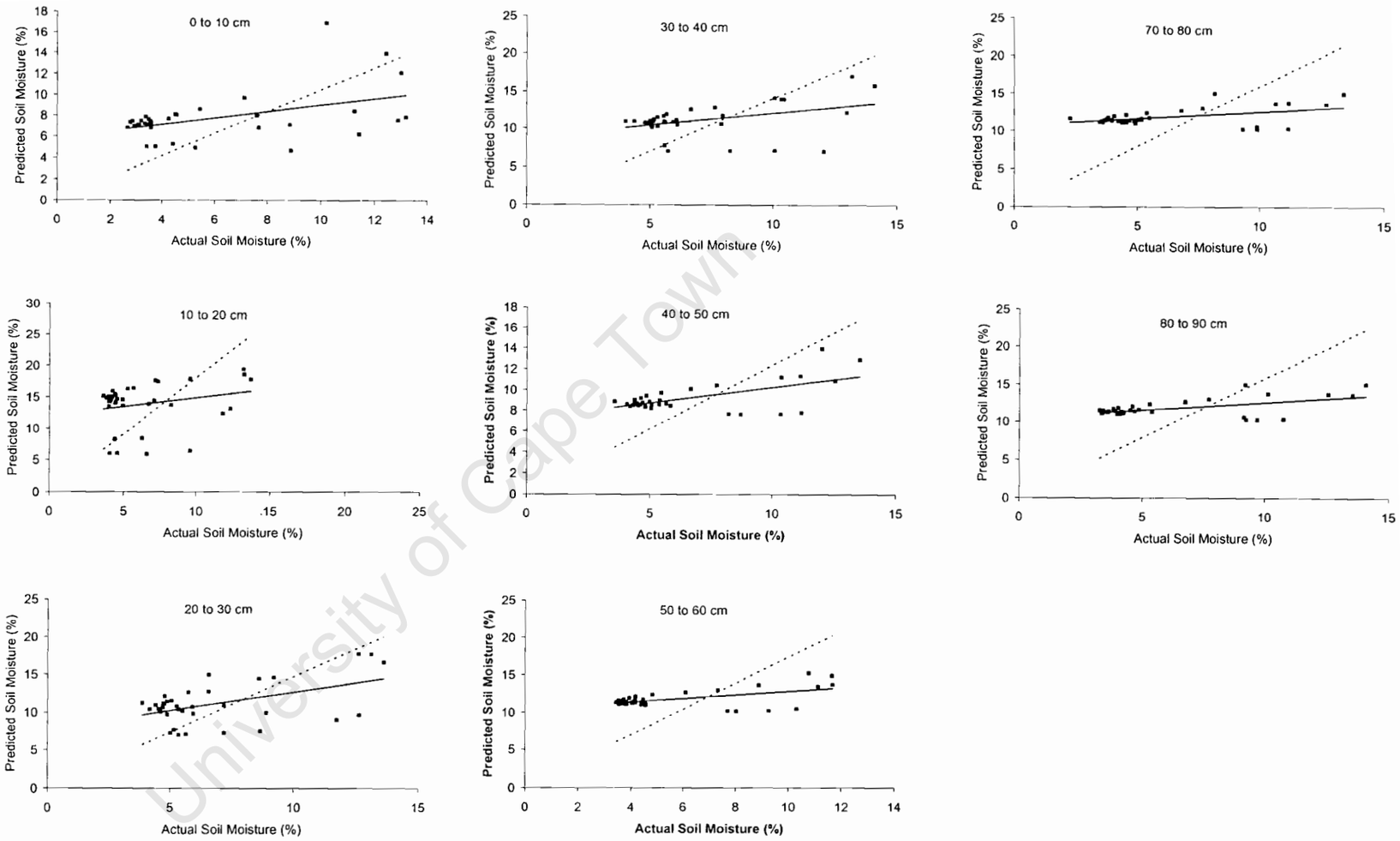

Figure 2 The relationship between predicted and measured soil moisture values for the granite sandy soil for the different depth layers. The dotted line indicates the regression line through the intercept.

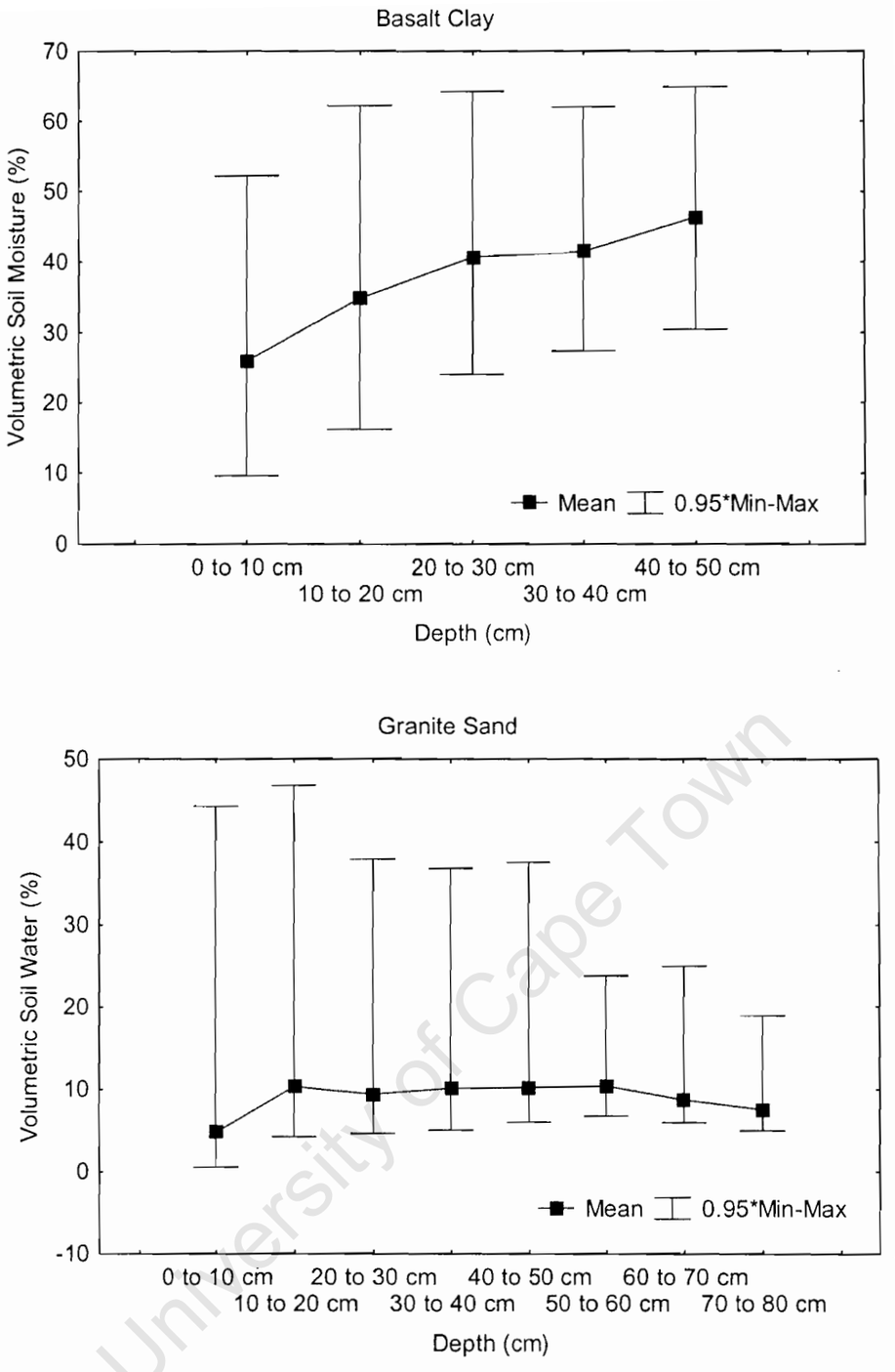

Figure 3 The average measured volumetric soil moisture (%) by depth for the Lower Sabie basalt clay and Pretoriuskop granite sand field experiment sites. Whisker plots indicate 95% of the minimum and maximum recorded values.

Table 1 The relationship between measured and predicted volumetric soil moisture for basalt clay and granite sand across all depths. The regression relationship between the measured and predicted soil moisture through the intercept are indicated as (0). The R-square values through the origin (no intercept) are not given since this value cannot be compared to the R-square value where the intercept is included.

Soil Depth	n	R^2	P - value	F - Ratio	P – value (0)	F – Ratio (0)
				Lower Sabie		
0 to 10 cm	39	0.51	0.0001	38.77	0.0001	431.91
10 to 20 cm	39	0.72	0.0001	94.10	0.0001	1087.87
20 to 30 cm	39	0.66	0.0001	70.92	0.0001	830.56
30 to 40 cm	39	0.62	0.0001	59.84	0.0001	903.43
40 to 50 cm	24	0.85	0.0001	128.64	0.0001	2002.04
				Pretoriuskop		
0 to 10 cm	34	0.22	0.005	9.20	0.0001	135.42
10 to 20 cm	34	0.06	0.156	2.11	0.0001	146.36
20 to 30 cm	34	0.25	0.0025	10.74	0.0001	272.21
30 to 40 cm	34	0.17	0.0155	6.52	0.0001	271.47
40 to 50 cm	34	0.38	0.0001	20.54	0.0001	275.85
50 to 60 cm	34	0.31	0.0005	14.92	0.0001	193.64
70 to 80 cm	34	0.23	0.0037	9.79	0.0001	178.34
80 to 90 cm	34	0.31	0.0006	14.54	0.0001	154.54

Defining the criteria for germination and seedling survival

Germination

I used the soil moisture conditions that stimulated germination at my Lower Sabie site to develop the criterion for germination. I used the 0 to 10 cm layer since the seeds were not planted deeper than 2 cm at the Lower Sabie basalt clay site and germination from deeper layers is not likely.

Figure 4 shows the total number of germinants at the Lower Sabie basalt clay study site for *Acacia nigrescens, Colophospermum mopane, Cassia abbreviata* and *Philenoptera violacea* for seeds planted on the 3rd of November 2002 (Chapter 4). Two main germination events were noted: the first 97 seedlings emerged on the 12th of December and the following 273 seedlings emerged on the 20th and 21st of December 2002 (Fig. 4; Chapter 4).

From petri dish and greenhouse experiments it appears that size and rate of germination is related to the amount and frequency of watering, increasing with increased irrigation frequency (Bebawi & Mohamed, 1982; Wilson & Witkowski, 1998) and less negative soil water potential (Choinski & Tuohy, 1991). Wilson and Witkowski (1998) report germination of *Acacia tortilis, Acacia karroo, Acacia nilotica* and *Mundulea sericea* after 10-14 days occurred only when the experimental pots were watered at their highest irrigation frequency of 16 ml every two days. Seeds under abundant moisture supply took only 5 – 10 days for radicle emergence (Wilson and Witkowski, 1998).

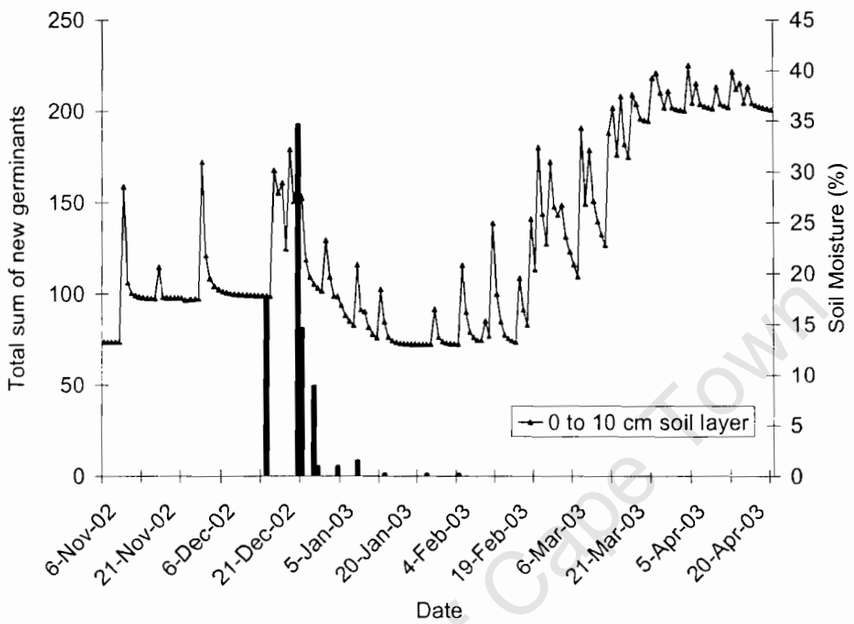

Figure 4 The measured volumetric soil water content of the 0 to 10 cm soil layer for the basalt field experiment site at Lower Sabie (Chapter 4) is depicted by the line graph. The columns show the total number of new germinants of *Acacia nigrescens, Philenoptera violacea, Colophospermum mopane* and *Cassia abbreviata* that was recorded per date. Seeds were planted at the end of October 2002. (Chapter 4)

Bebawi & Mohamed (1982) showed that six different *Acacia* species germinated best under daily irrigation, as opposed to three or six day cycles. Hypocotyls of *Combretum apiculatum, Acacia tortilis, Acacia karroo* and *Colophospermum mopane* emerged when kept in water for 4-5 days (Choinski & Tuohy, 1991). Seven days after major rainfall events were sufficient time for emergence of *Acacia karroo* in a field experiment (O'Connor, 1995).

The two largest germination events recorded at the Lower Sabie basalt clay site are possibly linked to the soil moisture regime directly prior to the time of germination. The size and rate of germination correlated with the soil moisture regime directly prior to the germination event. The first germination event was smaller and took longer because the soil moisture remained high for only a day, 17 days prior to the germination event (above 30% for one day followed by 17 consecutive days above 19%)(Fig. 4). Conversely the second germination event was bigger and occurred more rapidly because the soil moisture directly preceding the event remained higher for longer (above 28% for six consecutive days and never dropping below 23%, Fig. 4).

Apart from a trickle of germination until two weeks after the biggest germination event, no further germination was recorded at the Lower Sabie basalt clay site. This is despite the occurrence of increased soil moisture above 28% for the 0 to 10 cm layer for six consecutive days or more later during the season (Fig. 4). This lack of germination may be related to cues other than soil moisture. It is unlikely to be related to temperature since Choinski & Tuohy (1991) showed that *Acacia tortilis, Acacia karroo, Combretum apiculatum* and *Colophospermum mopane* have high percentage germination over a temperature range from 20 to 35°C. The average monthly temperatures for Lower Sabie and Satara have a much smaller temperature range over the growing season (Chapter 2). I found no research that suggests these species have specialized germination cues.

It is possible that no more germination events were recorded because the viable proportion of seeds had all germinated after the first favorable soil moisture conditions and thus no seed bank was available later during the season. The smaller germination events after the biggest germination event may be related to slightly different imbibition rates of the seeds due to varying levels of scarification. The small rainfall event at the start of November may have been too small to stimulate complete germination (Fig. 4).

Germinants after a small rainfall event may run a higher risk of mortality if no follow-up rain occurs. This is because smaller rainfall events will wet a shallower portion of the soil profile compared to larger rainfall events. However, if successful, germination after a small rainfall event may allow for establishment opportunities during dry years

in the absence of large rainfall periods (Watson *et al.,* 1997; Wiegand *et al.,* 2004). This form of bet-hedging (Clauss & Venable, 2000) will mean that seedling establishment could occur almost yearly, although the size of the establishment event may be smaller in low rainfall years (Wiegand *et al.,* 2004, Watson *et al.,* 1997).

Definition of successful germination

Given that germination is probable after small and larger rainfall events (Fig. 4), I define two sets of soil moisture conditions that potentially stimulate a large and small germination event respectively using the volumetric soil moisture data from the Lower Sabie experimental site.

High soil moisture germination event: Volumetric soil moisture should be above 28 % for the 0 to 10 cm soil layer for six or more consecutive days (Fig. 4).
Low soil moisture germination event: Volumetric soil moisture for the 0 to 10 cm soil layer should have a maximum of one day above 30 % followed by a period of 17 days or more above 19 % (Fig. 4).

Seedling survival

Root elongation

Once a seed has germinated the emerging radicle requires sufficient soil moisture to prevent mortality. The average age at which seedling mortality occurred after germination at the Lower Sabie basalt clay site was 16 days for *Philenoptera violacea* (n= 65) and 15 days for *Acacia nigrescens* (n = 35). I suspect that seedling mortality is high during this initial period after germination because seedling roots are pushing through a drying soil region (Chapter 4).

From the greenhouse experiment I measured that roots of both *Acacia nigrescens* (n = 13) and *Philenoptera violacea* (n = 25) seedlings grow 40 cm in twenty five days in basalt clay. The roots of the seedlings in the field experiment would thus have been in the 10 to 40 cm layer when mortality occurred. Using the model I determined the

average volumetric soil water content for the 10 to 40 cm soil layer at the Lower Sabie basalt clay site. I used these soil water content estimates to determine the average volumetric soil moisture content at which seedling mortality occurred in the field. The average soil water content of the 10 to 40 cm depth layer at which mortality was recorded was 28% for *Philenoptera violacea* and 30% for *Acacia nigrescens.*

Seedling survival

I make the assumption that water extraction by seedlings is possible throughout the soil profile. I therefore assume that seedlings are able to take up water by lateral roots from rainfall events that only wet the soil layers lying above the main taproot. Mortality should thus occur when the entire soil moisture profile drops below a threshold moisture level required for seedling water abstraction. The layer to dry out last will be the deepest layer (Fig. 3) and mortality should occur once this layer dries out unless a recharge event occurs in the shallow soil layers. At the Lower Sabie field experiment site, seedlings of *Acacia nigrescens* and *Philenoptera violacea* were able to survive an extended eleven month dry spell. The volumetric water content of the deepest soil layer (40 to 50 cm) never dropped below 32 % during this eleven month dry period (indicated by the minimum bar in Fig. 3). Again, it could be that mortality would not have occurred if this soil layer dried out to lower levels, but it is not possible to determine this.

Criteria for seedling survival

2. *Root elongation phase:* The second criterion I defined was that volumetric soil moisture for the 10 to 40 cm soil layer should not drop below 30 % for twenty five days after a period when the germination criterion was met.

3. *Root survival phase:* The third criterion was that the 40 – 50 cm layer should be above 32 % *for a period of time* after the second criterion for root elongation was met. *Successful root survival* is defined as the deepest layer remaining above 32 % until the start of the second wet season, the 1st of October.

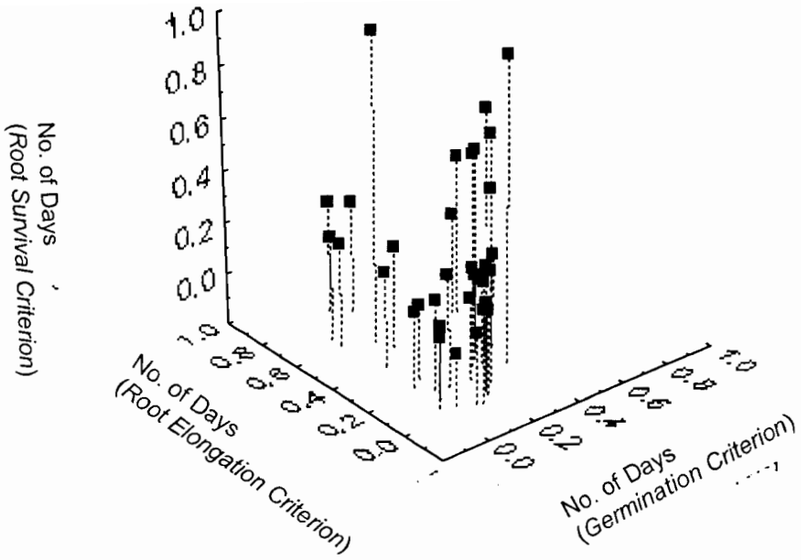

Figure 5 Graph showing the number of *high soil moisture establishment* events in the *presence of grass growth* for Satara. The number of days the *germination criterion* was fulfilled varied from seven to 105 (scaled from 0 to 1). The number of days the *root elongation criterion* was fulfilled varied from 31 to 112 days (scaled from 0 to 1). The number of days the root survival criterion remained above 32% varied from 133 to 713 days (scaled from 0 to 1).

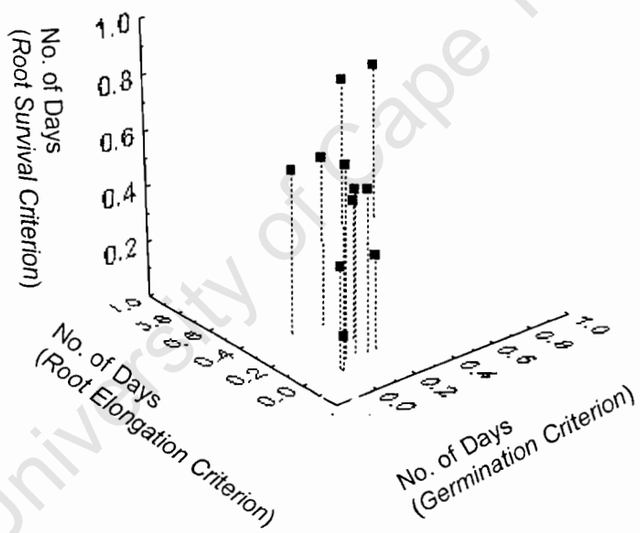

Figure 6 Graph showing the number of *high soil moisture establishment events* in the *absence of grass growth* for Satara. The number of days the *high soil moisture germination criterion* was fulfilled varied from six to 76 (scaled from 0 to 1). The number of days the *root elongation* criterion was fulfilled varied from 25 to 96 (scaled

from 0 to 1). The number of days the *root survival* criterion remained above 32% varied from 160 to 951 (scaled from 0 to 1).

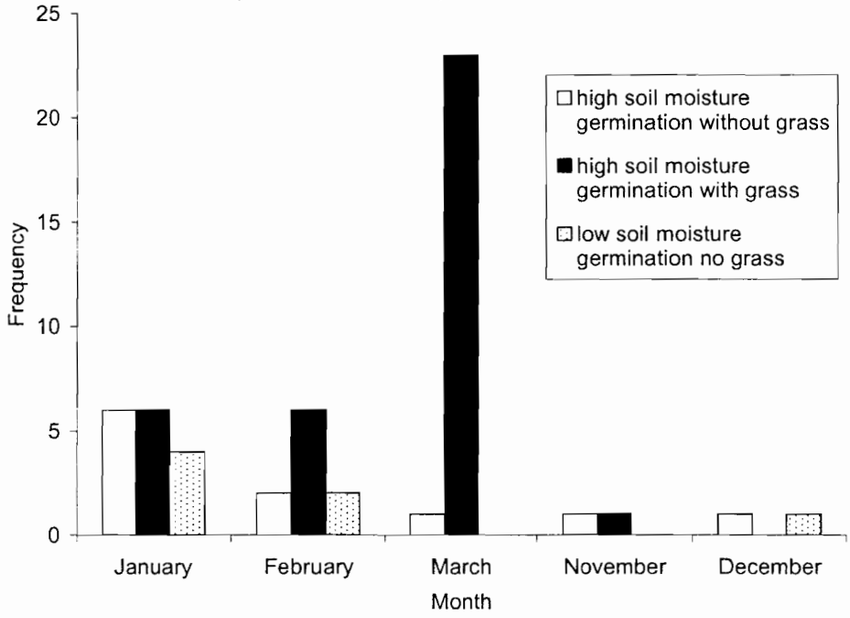

Figure 7 The number of events for which the *germination* and *root elongation* criteria were fulfilled estimated from 57 years of Satara rainfall data. Events are included irrespective of whether the *root survival* criterion was fulfilled.

Results

Soil moisture differences per depth layer with and without grass growth

Annual total soil evaporation was significantly higher ($p< 0.00$, $t_{1, 112} = 9.57$) and total annual grass transpiration significantly lower ($p< 0.00$, $t_{1, 112} = 4.59$) in the absence of grass growth. All three defined soil moisture layers were significantly wetter in the presence of grasses (Table 2).

Table 2 The mean predicted volumetric soil moisture (%) for three depth layers in the presence and absence of grass growth for 61 past Satara rainfall years for the whole year. Standard deviations are given in brackets.

Soil Depth Layer	With grass	No grass	P-value	df	F- ratio
0 to 10 cm	19.49 (5.02)	18.32 (3.96)	**	40 542	1.93
10 to 40 cm	26.27 (4.89)	25.68 (3.51)	**	40 542	1.61
40 to 50 cm	32.38 (4.61)	31.35 (3.32)	**	40 542	1.94

** is $P < 0.00$

The two criteria for seedling root elongation and survival are combined with the germination criterion for soil moisture conditions that would stimulate a) a large germination event and b) a small germination event, with and without grasses to determine how frequently successful seedling establishment may have occurred at Satara.

The results from the field experiment (Chapter 4) and other studies (Bebawi & Mohamed, 1982) suggest that the size of the germination event is related to the size of the rainfall event. For the purposes of the discussion it is assumed that the criterion defining a high soil moisture germination event has the potential to stimulate a larger germination event than the criterion that defines a small moisture germination event. Therefore a large germination event refers to the soil moisture conditions defined by the high soil moisture criterion.

High soil moisture germination event

With grass

Twenty six of the 57 rainfall years met the *high soil moisture germination* criterion followed by successful *root elongation* in the presence of grass growth (Fig 5). The two seedling establishment criteria were met more than once in eight of these years and in total 36 events fulfilled the *germination* and *root elongation* criteria (Fig 5). Only six years, 1942, 1980, 1981, 1984, 1996 and 2001 had establishment events

where the *root survival criterion* was fulfilled to the start of the next wet season (Table 2).

The largest variation in the mean total number of days where all three criteria were met was for the *root survival criterion* that varied from 133 to 713 days. To reduce the bias towards the *root survival criterion* the range of days for each criterion was scaled between zero and one. The product of the three soil moisture criteria values was used to indicate which possible establishment events had the most favorable soil moisture conditions. Using the product instead of the sum and standardizing the range of each criterion to fall between zero and one reduces the bias of the large range of days where the *root survival* criterion is fulfilled. The smallest possible establishment event occurred in March 2001 (product of 0.00 for all three axes) and the largest occurred in January 1996 (product of 0.28 for all three criteria) (Fig. 5).

The periods with the longest number of days (the sum of the number of days for all three criteria) (the tallest points in Fig. 5) is February 1980 and March 1980 with a total of 805 and 772 days where all three criteria are met (Fig. 5). Eighty nine percent of the total number of soil moisture days conducive for establishment for these two events was accounted for by soil moisture above 31.5 % for the 40 to 50 cm soil depth layer (Fig. 5).

The establishment events of February-March 1980 co-occurred with a tropical cyclone named Kolia that originated in the equatorial areas of the Indian Ocean and progressed only as far as the southernmost point of Madagascar (South African Weather Bureau). Another ten of the 36 possible establishment events occurred in synchrony with tropical cyclones that brought rain to southern Africa, all of which occurred in January, February or March. In total 12 tropical cyclones were reported by the South African Weather Bureau to have brought rain to the Kruger National Park between 1958 and 2002. An additional tropical cyclone brought rain to my field experiment sites at Lower Sabie and Pretoriuskop (Chapter 4) in 2003.

Without grass growth

In the absence of grass growth, 10 years (1936, 1942, 1946, 1949, 1955, 1956, 1958, 2000, 2002) and eleven periods had soil moisture conditions where the *high soil moisture germination* and the *root elongation* criteria were fulfilled (Fig. 6). Only the November 2001 event does not have successful *root survival*. The smallest possible establishment event occurred in March 1942 (product of 0.00 for all three axes) and the largest occurred in February 2000 (product of 0.59 for all three axes) (Fig. 6). The events occurred over the months from November to March with a peak in January (Fig. 7).

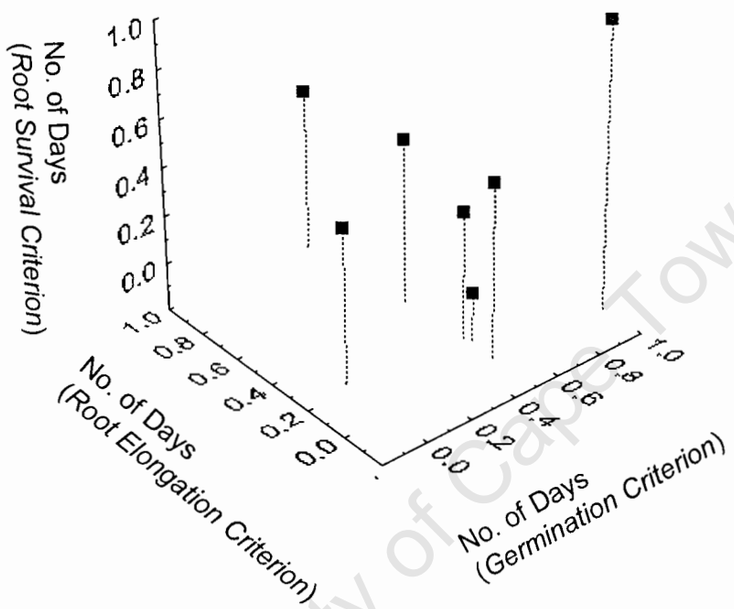

Figure 8 Graph showing the number of *low soil moisture establishment events* in the *absence of grass growth* for Satara. The number of days where the *low soil moisture criterion* was fulfilled ranged from 41 to 659 days (scaled from 0 to 1). The number of days where the *root elongation* criterion was fulfilled ranged from 25 to 96 days (scaled from 0 to 1). The number of days the *root survival* criterion was fulfilled ranged from 294 to 952 days (scaled from 0 to 1).

Low soil moisture germination event

With grass growth

In the presence of grass growth, no establishment events occurred for the *low soil moisture germination* and *root elongation* and *root survival* scenario. In total the low soil moisture criterion for germination was fulfilled 62 times, but the second criterion for successful *root elongation* was not fulfilled for any of these events and only four times for the *root survival* criterion.

Table 2 The number of times seedling establishment criteria were met for the four combinations of high/ low soil moisture and with and without grass growth. The table indicates the number of times the criteria for sufficient moisture for germination was met and the number and proportion (given in brackets) of those events for which sufficient moisture for root extension, and for survival through the dry season was met. The % of days out of the total 19 725 days that fulfilled the requirements for each criterion are presented.

	Germination criterion		Root elongation criterion		Root survival criterion	
	no. of events	no. of days (%)	no. of events	no. of days (%)	no. of events	no. of days (%)
High soil moisture with grass	107	0.1	39 (0.37)	0.1	6 (0.06)	0.13
High soil moisture without grass	86	0.05	11 (0.13)	0.02	10 (0.12)	0.29
Low soil moisture with grass	62	2.01	0		0	
Low soil moisture without grass	177	1.86	7 (0.04)	0.02	7 (0.04)	0.26

Without grass growth

In the absence of grass growth, six years (1949, 1958, 1975, 1996, 1999, 2000) and seven events fulfilled all three criteria of the *low soil moisture germination* and establishment scenario (Fig. 8). January 1958, January 1975 and February 1999 were the smallest (products of 0.00 for the three axes) and February 2000 was the largest establishment event (product of 0.23). Four of the seven possible establishment events occurred in January, two in February and one in December (Fig. 7).

Comparison between the four scenarios

High soil moisture germination events are more frequent with grasses than without grasses whereas *low soil moisture germination* events are more frequent without grasses (Table 2). Survival to the following wet season after a high or a small germination event is more frequent without grass growth (Table 2). The *root elongation* criterion is the most likely to fail (Table 2). For all of the four scenarios the total number of days that met the requirements for the *root elongation* criterion was met the least often (Table 2).

Discussion

With or without grass growth 16 events occurred in the last 57 Satara rainfall years where all three criteria for a large seedling establishment event were fulfilled. Combining suitable soil moisture conditions with factors like seed availability (Barnes, 2001; Coe & Coe, 1987; Miller, 1995), herbivory (Prins & van der Jeugd, 1993) or untimely fire (Hoffman, 1996; Williams, 1999) suggests that tree seedling establishment at this site is a comparatively rare event. On average, moisture conditions suitable for seedling establishment would occur about twice in a decade. Though seedling establishment is comparatively rare, it is much more frequent than the initiation of cohorts of saplings and trees (February *et al.*, 2006). Determining that tree seedling establishment is a relatively rare event at this site is an important finding. Before this study was done it was unknown whether the frequency of tree seedling establishment was once a decade or perhaps even once a century.

The prediction by Wiegand *et al.*, (2004) that large recruitment events should be rarer (1.6 per century) than smaller recruitment events (annual probability of 50 %) was not supported by this study. Only seven of the sixty one rainfall years had soil moisture conditions conducive for a small establishment event and only in the absence of grass growth. This equates to 11.5% small germination events per century compared to 26% for large establishment events.

Higher probability of a large tree seedling establishment event may be due to the common occurrence of tropical cyclones over the Indian Ocean that distributes a large

amount of rainfall over the Kruger National Park region. These tropical cyclones occur during January to March and provide enough rainfall for large moisture recharge of the deepest soil layer (Chapter 4). Therefore contrary to the prediction that germination at the start of the wet season should allow sufficient time for tree seedlings to grow root biomass to survive the subsequent dry season (Williams, 1999), establishment events at Satara had a high probability of occurring and surviving right at the end of the wet season in March. The big recharge of the 40 to 50 cm layer afforded by large rainfall events ensures seedlings roots are able to reach the deepest layer that is wetter than average and there is a smaller time period for this soil layer to dry out before the start of the following wet season in October.

This study is possibly the first to demonstrate what strategy savanna tree seedlings need follow to enable survival. Unlike succulents where survival is dependant on the amount of water-storage space that is developed during the first wet season and does not dry out before the start of the following wet season (Jordan and Nobel, 1979), survival of savanna tree seedlings on clay soil is dependant on the roots reaching a stable supply of water.

The classic equilibrium model of savannas ((Walter, 1971) suggests that trees and grasses co-exist because, although grasses are superior competitors for water in the upper soil profile, trees have preferential access to deeper water and are therefore able to persist in the system. It has been highlighted that the root-niche separation model (Walker & Noy-Meir, 1982) ignores the critical seedling phase of trees where they are probably accessing water over a similar layer to that of grasses (Sankaran *et al.*, 2004). My results suggest that the presence of grasses reduces the probability of tree seedling survival after both a large and small germination event (Table 2 & 3). However this is based on the assumption that grass root biomass is distributed in the upper soil layers. Weltzin & McPherson (1997) (Weltzin & McPherson, 1997)found that tree seedlings were utilizing water in the uppermost soil layers, whereas grass exploitation was from deeper layers. Although grasses may reduce the probability of soil moisture conditions conducive for seedling survival, they facilitate large (but not small) germination events, possibly by reducing soil evaporation (Table 2 and 3).

Seedling germination and survival criteria

The logic behind the development of the soil moisture criteria for seedling establishment forms the basis of determining the frequency of occurrence of possible establishment events. These criteria are based on assumptions which are naturally open to criticism. For example, the carbon stored in the cotyledons may allow seedlings to reach the deeper soil layers despite no rain following a germination event. In this case, they may not require a period of suitable soil moisture in the 0 to 40 cm soil layer to reach the 40 to 50 cm layer.

Criticism can also be leveled at the assumption that a seedling establishment event is not successful if the 40 to 50 cm soil layer dries to below 32 % volumetric soil moisture before the start of the second wet season. No dry season mortality occurred at the Lower Sabie basalt clay site where the soil 40 to 50 cm soil moisture layer did not drop below 32 % for 11 dry months without rain. The volumetric soil water at which mortality occurs may be much lower than 32 % and the 40 to 50 cm layer may never drop to a volumetric soil water content that would cause mortality to seedlings (Fig. 3).

The possible establishment events are therefore represented (Fig. 5, 6 and 8) without omitting those years where the 40 to 50 cm layer dries to below 32 % before the start of the second wet season. It does however indicate that for a large proportion of the establishment events, the length of favorable soil moisture conditions in the deepest layer does not endure to the start of the following rainy season.

For the model, the parameter pertaining to grass root biomass was defined so that 50 % of the grass root biomass occurs in the top 24 cm (based on personal observation). Changing this depth may influence rate of transpiration and therefore the frequency of possible establishment events.

Predictions

It was not possible to test how differences in soil substrate influence establishment frequency because of the poor predictive power for the granite sand. Never the less,

the results of the verification of the soil-water model highlight the hydraulic conductivity and water retention differences between the granite sand and basalt clay soil types. These results suggest that a different set of criteria are required for survival of tree seedlings on granite sand compared to basalt clay (Chapter 4). Species with taproots will not reach moister more stable soil moistures with depth on the granite sands. Instead, thickening roots by storage of nutrients and water may allow seedling survival on granite sands by providing resources for the seedling to resprout after dry periods (Oliveira & Silva, 1993). In this case, survival will be proportional to the number of growth days the seedling has received (Chapter 5).

Conclusion

This paper suggests how you could logically dissect the problem of determining the frequency of savanna tree seedling establishment and perhaps for the first time produced a model of how to predict suitable seedling establishment for trees. It further illustrated which phase of seedling growth is the most important for seedling survival. Existing hypotheses suggested that the length of the dry season and the time seedlings had to grow were critical to seedling survival. The results from this study suggest that soil moisture conditions suitable for dry season survival (*root survival* criterion) were the most frequently met. Instead, receiving follow-up rain following a germination event to ensure soil moisture conditions suitable for successful *root elongation* is the criterion that is most likely not to be met (Table 2). This study suggests that a combination of large, more frequent and small, less frequent tree seedling establishment events have occurred at Satara. The increased soil moisture with depth and the stable nature of the deepest soil layer improves seedling survival on basalt clay despite low rainfall of the site. A total of 37.5 % (11.5 % small and 26 % large) small and large establishment events in the presence and absence of grasses were possible over the past 57 years at Satara. The rare observation of seedling recruitment at this site (A. Potgieter, *unpubl. data*) suggests seedling establishment is limited less by suitable soil moisture conditions than by other factors such as seed availability, or injury to seedlings from browsing and fire (Chapter 4).

Chapter 7

Conclusion

The research presented in this thesis is significant because it indicates that many of the assumptions of seedling survival of savanna tree species are incorrect. For one, the suggestion that savanna tree seeds should germinate at the start of the wet season because this will enhance dry season survival was not supported for species grown on basalt clay. The length of the rainy season has been shown to increase the survival of desert succulents because it increases the water-storing leaves they can grow (Jordan & Nobel, 1979). Here survival is enhanced if the water-storing leaves are big enough not to completely dehydrate before the start of the following wet season. However results from my field study showed that no difference existed in dry season seedling survival for two savanna tree species that had received different growing season lengths. Furthermore unlike desert succulents (Jordan & Nobel, 1979) survival of species grown on basalt clay was not related to seedling size. The results indicated that survival of savanna species grown on basalt clay is related more to reaching water than to storing water. Survival depends on taproots reaching deeper, moister soil layers which do not dry out below a critical threshold.

However results from my greenhouse study suggests that wet season length should increase dry season survival for some species that grow on sandy soils. Unlike the species grown on basalt clay, species grown in granite sand survived significantly longer dry spells with increased seedling size. This suggests that dry season seedling survival may be related to wet season length for species grown on sandy soils, although low germination in the field experiment prevented me from testing this. These results suggest that strategies for surviving dry spells differ depending on soil type. Species that grow on sandy soils may grow water-storing roots combined with, or instead of, deep taproots since soil water content does not increase with depth on the granite sand. Swollen parts of taproots just beneath the soil surface have been observed for seedlings of *Pterocarpus angolensis* and *Adansonia digitata* (*S. Botha, pers. observation*). Saplings with no taproots have also been observed for *Terminalia sericea* that dominate on the granite sand area of Pretoriuskop (*L. Rademan, pers.*

comm.). Interesting, too, that *Sclerocarya birrea* has thick, swollen, fleshy taproots. So much so that it was targeted by monkeys at Pretoriuskop.

I also investigated whether tree species cue their germination to occur at the start of the wet season since this would maximize the length of the wet season they have to grow. Preliminary results from a germination experiment suggest that seed of some species could germinate in any given month. However large germination events are more probable after large rainfall episodes, which have the highest likelihood of occurring towards the middle and middle-end of the rainy season for Pretoriuskop and Satara respectively. This was substantiated by a large germination event recorded for *Terminalia sericea* towards the middle of the rainy season in the Pretoriuskop area. The lack of field germination, the absence of a seed bank and the germination of added seed at the field experiment site after rainfall emphasizes seed limitation as an important bottleneck at Satara (Midgley & Bond, 2001). Browsing is much greater around the Satara area than Pretoriuskop and browsing, particularly by giraffe on *Acacia nigrescens* which dominates around the Satara area, should impact significantly on seed production (Miller, 1995). The effect of browsing is ignored in the "tree demographic model" of co-existence by trees and grasses and emphasis is placed on variable rainfall limiting tree density in xeric savannas (Higgins *et al.*, 2000).

However the findings from this thesis suggest that the co-existence of trees and grasses at my semi-arid site is not related to increased rainfall variability. No significant difference in rainfall variability, despite significantly different annual rainfall, was found for my two study sites within the Kruger National Park. Furthermore rainfall conditions suitable for germination and seedling survival did not occur more frequently in the past at Pretoriuskop compared to Satara.

This is supported by the finding that seedling recruitment at the Satara area can occur at least twice a decade, which should be frequent enough to allow a transition to a woodland state over time. Determining the frequency of recruitment for some species that grow around Satara contributes greatly to our understanding of the importance of the seedling phase as a bottleneck to tree establishment. For example, the observed frequency of large recruitment events is much rarer than once every five years (*A.*

Potgieter, unpubl. data) for species in the Satara region which implies that a mechanism other than rainfall variability is driving the co-existence of trees and grasses at the semi-arid site.

Before this study it was also not known how frequently the right rainfall conditions suited for seedling establishment occurred; e.g. whether it was once every ten years or once every 100 years. The similarity in seedling response to drought stress between two species with very different leaf morphologies also suggests that soil moisture regimes are more important in determining tree recruitment intervals on basalt clay than seedling morphology.

The difficulty in modeling the soil moisture regime of granite sand prevented determining the recruitment frequency for species that grow on these soils. A different model is required for determining recruitment frequency for species grown on granite sand since seedling size increased with the number of growth days.

The results from this thesis are surprising since they suggest that sufficient rainfall during the seedling recruitment phase is not more critical in a semi-arid compared to a semi-mesic savanna. Whereas more frequent fire is important in preventing escape opportunities for tree saplings in mesic savannas (Higgins *et al.*, 2000) browsing of seed and seedlings (Prins & van der Jeugd, 1993) may be more important in xeric nutrient-rich savannas.

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Appendix A – Description and values of parameters used in WaterMod

Soil hydraulic characteristics were kindly obtained from the Tree-Grass Project who conducted soil hydraulic profiles for Satara and Pretoriuskop. Standing grass biomass is included in the model and is calculated to be a function of annual rainfall. Temperature, average wind speed and relative humidity that are required for WaterMod3 calculations were obtained from the permanent weather stations positioned within the rest camps at these two sites. The data from these stations are available from the South African Weather Services. The remaining climatic variables like day length were calculated internally by WATERMOD (see below for specific details).

The parameters used by WaterMod for running simulations are divided into three modules, climate, soil and crop which are discussed below. The values used for the parameters for Lower Sabie and Pretoriuskop are given in table 1.

Climate Module

Daily rainfall data
Daily rainfall distribution
Temperatures (mean Min (C), mean Max (C), Date of max, Diurnal Range (C))
Soil Temperature (Mean Min (C), Mean Max (C), Date of Max)
Soil water content with depth (% v)
Clear sky conditions (Atmospheric transmissivity, % of potential)
Net radiation (net solar radiation during daylight)
Albedo (%) (Green albedo, Dead/litter albedo, Wet soil albedo)
Relative humidity (Mean Min RH (%), Mean Max RH (%), Date of max, Diurnal range)
Wind-speed (Mean daily wind-speed (m/s))
Day length (latitude)
Potential Evapotranspiration (Full Penman-Monteith or standard reference ET)

C_3 or C_4 crops

Crop Growth Module

Growth

Leaf Pmax at optimum temperature (mg $CO_2/m^2.s$)

Pmax temperature (C) (Min, Optimum, Max)

Curvature for Pmax (sets the slope of the curve of Pmax to Temp)

Growth Characteristics (Date of Emergence, Number of days from emergence to anthesis, Number of days from anthesis to maturity)

Light extinction coefficient (a value between 0 and 1)

Roots

Root distribution (sigmoidal or exponential)

Maximum root depth (cm)

Depth for 50% root distribution

Scale factor (a value between 1 and 10)

Transpiration:

The extent to which there is compensation for dry soil regions by wetter regions (from none to full, as a percentage)

Soil Water Growth Limiting Factor (GLF) (defines the shape of the graph depicting the growth limiting factor in response to soil water content)

Litter

Rate constant for litter decay (%/day)

Q10

Initial litter dry weight (t/ha)

Soil-Water module

Soil-physical properties

Infiltration model (Capacitance or Richard's equation)

Depths for four layers of the soil profile from surface to the soil profile depth

The generic soil type for each of the four profiles (user defined, sand, sand clay, loam, sandy clay loam, sandy loam, loamy sand, clay loam or clay)

Saturated water content (% volumetric) for each of the four soil profiles

Ksat (cm/d) for each of the four soil profiles

Field capacity (-100cm) (%v) for each of the four soil profiles

Wilting point (-150cm) (%v) for each of the four soil profiles

Physical properties (Campbell equation or user defined)

Wet up or dry down

Infiltration time-step factor

Initial soil-water content

Canopy and litter water interception ((Maximum LAI water storage capacity (mm of water)/ LAI and Litter water storage capacity, mm (t / ha))

Litter dry weight (t/ha) for 50% reduction in evaporation

Run-off

Profile characteristics (profile length (m) and profile inclination (%))

Bare soil surface water storage capacity (detention) (mm)

Bare soil flow constant (/sec)

Full ground cover flow constant (/sec)

Description of the parameters

Climate Module

Daily rainfall data

Where possible the actual rainfall data for the specific time frame the simulation was run, was used.

Daily rainfall distribution

This option spreads the rainfall equally across a specified numbers of hours a day, starting at a random time in the day. In the Kruger National Park, rainfall is often discreet events, typically thunderstorms that last from a few minutes to a few hours (du Toit et al., 2003). This option was set at one hour for Lower Sabie and Satara and at two hours for Pretoriuskop.

Temperature

Temperature data was extracted from the weather records for Lower Sabie, Pretoriuskop and Satara.

Soil Temperature

Some measurements with a soil temperature gun showed that bare basalt soil can be up to 20 degrees warmer than maximum air temperature. Soil temperature was set at 8 degrees higher than the average mean max air temperature for Pretoriuskop and at 12 degrees for Lower Sabie and Satara. Maximum soil temperature date was set to coincide with the date of maximum air temperature.

Clear Sky Conditions

Clear sky conditions are estimated from atmospheric transmissivity (value between 0 and 1) and percent of potential (percentage between 0 and 100). Transmissivity is a function principally of the aerosol optical thickness and is affected particularly in winter by the dust and smoke from wildfires (du Toit *et al.,* 2003). Average percent cloud cover recorded for Skukuza from 1961-1990 average 38.15 % per year (du Toit *et al.; 2003*). Skukuza, Lower Sabie and Pretoriuskop should generally have similar transmissivity values, whereas Satara is sunnier. Lower Sabie and Pretoriuskop were given atmospheric values of 4 and Satara a value of 2.

Net Radiation

Incoming shortwave radiation is calculated from the mean number of daily sun hours recorded for Skukuza from 1960-1990 (du Toit *et al.,* 2003) using the Angstrom relation and calibrating it with a radiometer positioned 120 km southwest at Nelspruit and averages 17.88 MJ/day.

% Albedo

Albedo is an indicator of the reflectivity of an object and is the ratio of the amount of light reflected by a surface to the light falling onto it, with snow typically having an albedo of 1 and charcoal around 0.04. The % albedo reference values of 23, 30 and 13 for respectively green, dead/litter and wet soil provided by Watermod 3 were kept the same for Pretoriuskop and changed to 23, 28 and 8 for Satara and to 23, 30 and 8 for Lower Sabie. This is because there is generally less dead/litter biomass at Satara and basalt clay soils are darker in colour than granite soils.

Relative humidity

Relative humidity (%) is the ratio of the amount of the actual water vapor in the air (absolute humidity) compared to the amount of water vapor the air can hold at that temperature and pressure, expressed as a percentage. Percentage relative humidity was extracted from the weather records for Pretoriuskop, Satara and Lower Sabie.

Wind-speed

Mean daily wind-speed (m/s) was extracted from the weather records for Pretoriuskop, Satara and Lower Sabie.

Day length

Day length is calculated automatically by Watermod from latitude values.

Potential Evapotranspiration

Potential evapotranspiration is a measure of the ability of the atmosphere to remove water from the surface through the processes of evaporation and transpiration assuming no limitation on water supply. In Watermod the choice lies between the Full-Penman Monteith equation that calculates values for four different components: values for potential transpiration, potential evaporation (green), potential evaporation (brown) and potential evaporation (wet soil), whereas only a single value is calculated with the simpler FAQ version.

The Full-Penman Monteith equation was used for all simulations.

C_3 or C_4 crops

The C_3 crop option was selected for the Lower Sabie run and C_4 for Satara and Pretoriuskop.

Crop Growth Module

Leaf Pmax

Pmax is defined as the rate of single leaf gross photosynthesis at saturating irradiance and optimum temperature. Pmax is strongly temperature dependant with C_3 plants typically having an optimum Pmax at a temperature of 20 °C declining at higher temperatures and typical C_4 plants reaching an optimum at 30

°C onwards. Setting the function to the default C_3 option sets the Pmax min temperature at 0°C, Pmax optimum temperature at 20°C and Pmax maximum temperature at 30°C. The default C_4 option sets Pmax minimum temperature at 0°C, Pmax optimum temperature at 20°C with no Pmax value applicable. Leaf Pmax at optimum temperature (mg CO_2 / (m^2.s)) is a value between 0.1 and 5, and the default option is 1. The curvature for Pmax option defines the steepness of the slope of the curve depicting Pmax to temperature and is an option between 0.1 and 5, with the default setting being 2.

Growth Characteristics

The only phases that are considered are vegetative (from germination to anthesis) and reproductive (from anthesis to maturity). Germination is specified as a date.

Light extinction coefficient

Light interception by the leaves in the canopy is described by Beer's law, which defines the attenuation of light through the canopy by a simple exponential decay. The only parameter to describe the light attenuation in WaterMod is the light extinction coefficient (m^2 ground) (m^2 leaf)$^{-1}$. The extinction coefficient typically increases as leaf orientation becomes more horizontal with cereals averaging 0.5 and broad-leaf plants 0.8.

Roots

The root distribution describes the shape of the curve (sigmoidal or exponential) defining the relative root distribution to depth. The sigmoidal curve allows for a larger percentage of the roots to be concentrated in the upper soil layers. The scale factor between 1 and 10 defines the slope of the sigmoidal curve with increasing values changing the slope such that a higher proportion of roots are in the upper

soil layers. The maximum root depth as well as the depth at which 50% of the root distribution occurs is defined in cm.

Transpiration

A graph depicts the growth limiting factor for water (GLF_{water}) in relation to the available soil water. If GLF_{water} is zero there is total limitation to growth and at one there is no limitation to growth. The GLF_{water} is defined in terms of four points on the soil water content axis, θ_w (wilting point), θ_r (recharge point), θ_{fc} (field capacity), θ_s (saturated water content).The recharge point (θ_r) is defined as the point at which irrigation would have to be applied in order to prevent any water status. GLF_{water} is zero below wilting point (θ_w), increases from 0 to 1 between θ_w and θ_r and remains at one between θ_r and θ_{fc}. Between θ_{fc} and θ_s, GLF_{water} may decline depending if plants are susceptible to water logging that inhibits their growth ability.

Litter

The initial dry weight (t/ha) defines the amount of litter present at the beginning of the simulation. This then decays according to the temperature and water status in the top soil layer. The rate constant for litter decay (%/day) (between 0 and 20) defines the proportion of litter that decays each day. The temperature response for the rate constant is described using the a Q_{10} factor.

Soil Water Module

Soil Physical Properties

This module sets the parameters that govern the behaviour of the movement of water in the soil i.e. infiltration and redistribution. In WaterMod the infiltration model is described either by Richard's equation or the Capacitance's model. Both solve for water distribution through the soil profile and have similar parametric inputs. The Capacitance model is described as being simpler and more robust, especially when dealing with strongly duplex soils. It is further described as numerically quicker and stable and should be useful when the general behaviour of the system is explored.

The soil characteristics can be defined for four layers in the soil profile, the surface layer, A horizon, B1 horizon and B2 horizon. The depth of the B2 horizon defines the depth of the profile. The generic soil type, saturated water content (%v), Ksat (cm/d), field capacity (-100cm) (%v), wilting point (-150cm) (%v) and air dry water content (%v) is defined for each of these layers.

The generic soil types can be user defined or selected from one of the following options: sand, sand clay, loam, sandy clay loam, sandy loam, loamy sand, clay loam or clay.

Saturated water content is defined as the maximum soil water content. This is generally the soil water content when all the air spaces are filled with water.

Saturated hydraulic conductivity (Ksat) is the flux of water through freely draining saturated soil.

Field Capacity is defined as the soil water content at –10kPa. It is generally regarded as the point at which freely draining soil will drain in a few days or so.

Wilting Point is defined as the soil water content at which plants are unable to move water. It is the soil water content at a suction of –1.5MPa.

Air Dry Water Content is defined as the soil water content at a suction of –20MPa.

Wet-up, dry-down

This option allows one to get an impression of the general behaviour of the profile by looking at situations when your profile is wetted from extremely dry, or dried from saturation.

Infiltration time-step

The model attempts to calculate the appropriate time-step for the calculations required, but sometimes, this needs refining, particularly for strongly duplex soils. By looking at the dry-down simulation and steadily increasing the infiltration time step-factor one can observe whether any irregularities whilst the soil profile is drying out.

Initial soil water content

This option sets the initial soil water content at the beginning of the simulation.

Canopy and Litter Water Interception

Plant canopy, leaves and dead litter can significantly influence overall water balance by intercepting water that is then evaporated directly without reaching the soil surface or alternatively shading the soil to prevent evaporation.

For canopy and litter evaporation the parameters are defined as; canopy (maximum) water holding capacity (mm water/ LAI) (a value between 0 and 10) and standing dead and litter water holding capacity (mm water/ (t/ha)) (a value between 0 and 100). Water in excess of the holding capacity of the canopy and litter is transferred to the soil surface and is available for infiltration.

Table 1 The parameter values used in the computation of soil water for the past rainfall years of Satara. For Pretoriuskop the values for the run that gave the best fit between observed and measured volumetric soil moisture is given.

	Satara	**Pretoriuskop**
Climate Module		
Daily Rainfall	*data file*	*data file*
Daily rainfall distribution	1	2
Max Temp	44.8	27.4
Min Temp	16.3	14.9
Diurnal Range	14.21	12.54
Date of Max Temp	27th January	15th January
Max Rel Humidity (%)	79.17	80
Min Rel Humidity (%)	49.75	40
Diurnal Range (%)	32.18	20
Date of Max Rel Humidity	27th of April	21st of April
Wind-Speed (m/s)	2.25	2
Latitude	-25.1	-25.1
Max Soil Temp	57	36
Date of Max Soil Temp	27th January	15th of January
Clear Sky Conditions	0.4	0.2
Net Radiation		
%Albedo:		
Green	23	23
Dead/litter	30	30
Wet Soil	8	13
C3 or C4 plants	C4	C4
Crop Growth Module		
Leaf Pmax Min Temp	0	10
Pmax Optim Temp	30	30
Pmax Max Temp	n/a	n/a
Leaf Pmax at Optimum Temp	1.2	1.2
Curvature for Pmax	2	2
Growth Characteristics		
Germination	21st of December	1st of November
Germination to anthesis	19th of February	31st of January
Anthesis to maturity	19th of April	1st of April
Light Extinction coefficient	0.7	0.7
Percent of potential solar radiation	80	80
Roots		
Root distribution model	exponential	sigmoidal
Max Root Depth (cm)	45 cm	90 cm
Depth of 50% Root Distribution (cm)	24 cm	30 cm
Root Distribution Scale Factor		5
Transpiration:		
Extent to which there is compensation for dry soil regions by wetter regions	50%	50%
GLF Shape parameter	0.4	0.4
Growth Limiting Factor for Water	0.8	0.8
Litter		

Initial Dry Weight (t/ha)	1	1
Rate constant for litter decay	0.7	1
Q10	3	2
Soil Water Module		
Infiltration model	Richards equation	Richards equation
Soil Characteristics		
Depth:		
Surface Layer	10	5
A horizon	20	10
B1 horizon	30	50
B2 horizon	50	90
Generic soil type		
Saturated Water Content (%)		
Surface Layer	55	37
A horizon	60	39
B1 horizon	65	30
B2 horizon	68	25
Ksat (cm/d)		
Surface Layer	111	400
A horizon	65	760
B1 horizon	55	488
B2 horizon	15	300
Field Capacity (-100cm)(%v)		
Surface Layer	30	16
A horizon	35	12
B1 horizon	37	17
B2 horizon	49	12
Wilting Point (-150 cm)(%v)		
Surface Layer	14	5
A horizon	17	6
B1 horizon	20	7
B2 horizon	25	7
Air Dry Water Content (%v)		
Surface Layer	9	2
A horizon	11	2
B1 horizon	19	3
B2 horizon	28	3
Initial Soil Water Content	Calculated by WaterMod	Calculated by WaterMod
Canopy and Litter Water Interception		
Max Canopy Water Holding Capacity (mm water/LAI)	1	0
Standing Dead and Litter Water Holding Capacity (mm water/ (t/ha))	10	10
Litter Dry Weight (t/ha) for 50% reduction evaporation	10	4
Runoff		
Profile length (m)	30	100
Profile Inclination (%)	5	5
Bare Soil Surface Water storage Capacity (mm)	3	6
Bare Soil Flow Constant (/sec)	50	70
Full ground cover flow constant (/sec)	5	5

Appendix A